Paleoecologic and Biostratigraphic Significance of Trace Fossils from Shallow- to Marginal-Marine Environments from the Middle Cambrian (Stage 5) of Jordan

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Abstract: The Hanneh Member (Cambrian Stage 5) of the Burj Formation and the Umm Ishrin Formation of Jordan represent a transgressive-regressive succession that contains twenty-eight ichnotaxa, including vertical burrows (Arenicolites isp., Diplocraterion isp., Gyrolithes polonicus, Rosselia isp., Skolithos linearis, escape trace fossils), horizontal simple burrows and trails (Archaeonassa fossulata, Gordia marina, Helminthoidichnites tenuis, Palaeophycus tubularis, Planolites beverleyensis, P. montanus), plug-shaped burrows (Bergaueria sucta), horizontal branched burrows (Asterosoma isp., Phycodes isp., Treptichnus cf. T. pedum), bilobate structures (various ichnospecies of Cruziana and Rusophycus), and trackways and scratch marks (Diplichnites isp., Dimorphichnus cf. D. obliquus, Monomorphichnus isp.). Eleven trace-fossil assemblages are identified. The Arenicolites isp. and Diplocraterion isp. assemblages occur in transgressive tidal dunes and bars whereas the Rosselia isp. assemblage characterizes areas between tidal dunes. The Cruziana salomonis assemblage reflects a wide variety of environmental settings including channels within tidal-bar complexes, bottomsets of tidal dunes, and interdune areas. The Gordia marina assemblage is present between dune patches. The Gyrolithes polonicus assemblage penetrates into firmground mudstone below the maximum flooding surface. The Bergaueria sucta, Archaeonassa fossulata, Rusophycus aegypticus and Cruziana problematica assemblages occur in different subenvironments of the progradational delta. Cruziana salomonis and Rusophycus burjensis, originally considered indicative of an early Cambrian age, are actually middle Cambrian in their type locality. Occurrences of Cruziana jordanica and Rusophycus aegypticus provide evidence that these ichnospecies are of the same age in Jordan and may co-exist in terms of stratigraphic distribution with C. salomonis and R. burjensis.

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PALEOECOLOGIC AND BIOSTRATIGRAPHIC SIGNIFICANCE OF TRACE FOSSILS FROM SHALLOW- TO MARGINAL-MARINE ENVIRONMENTS FROM THE MIDDLE CAMBRIAN (STAGE 5) OF JORDAN

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ABSTRACT—The Hanneh Member (Cambrian Stage 5) of the Burj Formation and the Umm Ishrin Formation of Jordan represent a transgressive-regressive succession that contains twenty-eight ichnotaxa, including vertical burrows (*Arenicolites* isp., *Diplocraterion* isp., *Gyrolithes polonicus*, *Rosselia* isp., *Skolithos linearis*, escape trace fossils), horizontal simple burrows and trails (*Archaeonassa fossulata*, *Gordia marina*, *Helminthoidichnites tenuis*, *Palaeophycus tubularis*, *Planolites beverleyensis*, *P. montanus*), plug-shaped burrows (*Bergaueria sucta*), horizontal branched burrows (*Asterosoma* isp., *Phycodes* isp., *Treptichnus* cf. *T. pedum*), bilobate structures (various ichnospecies of *Cruziana* and *Rusophycus*), and trackways and scratch marks (*Diplichnites* isp., *Dimorphichnus* cf. *D. obliquus*, *Monomorphichnus* isp.). Eleven trace-fossil assemblages are identified. The *Arenicolites* isp. and *Diplocraterion* isp. assemblages occur in transgressive tidal dunes and bars whereas the *Rosselia* isp. assemblage characterizes areas between tidal dunes. The *Cruziana salomonis* assemblage reflects a wide variety of environmental settings including channels within tidal-bar complexes, bottomsets of tidal dunes, and interdune areas. The *Gordia marina* assemblage is present between dune patches. The *Gyrolithes polonicus* assemblage penetrates into firmground mudstone below the maximum flooding surface. The *Bergaueria sucta*, *Archaeonassa fossulata*, *Rusophycus aegypticus* and *Cruziana problematica* assemblages occur in different subenvironments of the progradational delta. *Cruziana salomonis* and *Rusophycus burjensis*, originally considered indicative of an early Cambrian age, are actually middle Cambrian in their type locality. Occurrences of *Cruziana jordanica* and *Rusophycus aegypticus* provide evidence that these ichnospecies are of the same age in Jordan and may co-exist in terms of stratigraphic distribution with *C. salomonis* and *R. burjensis*.

INTRODUCTION

CAMBRIAN OUTCROPS containing abundant trace fossils are widespread in the southern Dead Sea area of Jordan (Fig. 1). Although some trilobite trace fossils have been mentioned in the context of the *Cruziana* stratigraphy (Seilacher, 1970, 1992), no documentation and detailed systematic analysis of ichnofaunas from this region within their sedimentologic and stratigraphic framework is yet available. The Hanneh Member (Cambrian Series 3, Stage 5) of the Burj Formation and the overlying Umm Ishrin Formation contain a number of trace-fossil assemblages that reveal a complex mosaic of subenvironments within a shallow- to marginal-marine clastic low-latitude setting. Excellent preservation of both trace fossils and physical sedimentary structures favors the detailed integration of ichnologic and sedimentologic datasets. This ichnofauna allows us to evaluate the response of the benthic fauna to stress factors in a tide-dominated transgressive tidal-dune and bar complex and a regressive deltaic environment. The aims of this paper are to: 1) document the ichnofaunas from the Hanneh Member and its transition to the Umm Ishrin Formation; 2) discuss trace-fossil distribution in the different subenvironments within a sequence-stratigraphic framework; 3) evaluate the paleoecologic and paleoenvironmental significance of these ichnofaunas; and 4) briefly address their implications for the *Cruziana* stratigraphy.

GEOLOGIC AND STRATIGRAPHIC BACKGROUND

The study area is situated at the southern end of the Dead Sea within the Jordan Rift Valley which, as one branch of an inferred late Proterozoic to early Paleozoic triple junction, separates the Arabian plate and the Turkish plate (Husseini, 1989; Schneider et al., 2007) (Fig. 1). Due to a significant sea-level rise near the end of the early Cambrian, the area was flooded for a short time. By the Furongian (late Cambrian), regression was already underway in the Jordan Rift Valley (Sharland et al., 2001). These authors assigned the related processes to a first-order transgressive-regressive cycle of the Cambrian–Ordovician "tectonostratigraphic megasequence" that affected the Arabian plate.

The Cambrian strata of southwestern Jordan non-conformably overlie Precambrian metamorphic and magmatic rocks of the Arabo-Nubian Shield (Aqaba Complex), or are in disconformable contact with Neoproterozoic volcanoclastics and conglomerates (Araba Complex; Bender, 1974; Powell, 1989; Teimeh et al., 1990; Jarrar et al., 1991; Bandel and Shinaq, 2003) (Fig. 2). The oldest Cambrian strata (parts of the Umm Ghaddah and Salib formations) are more than 200 m thick and are interpreted as continental, mainly alluvial deposits (Powell, 1989; Amireh et al., 1994, 2008; Makhlouf, 2003). The overlying Burj Formation (Cambrian Series 2 to 3) consists of three members (Tayan, Numayri and Hanneh) recording marine flooding on the Arabo-Nubian shield (Bender, 1974; Amireh et al., 1994; Rushton and Powell, 1998; Schneider et al., 2007; Shinaq and Elicki, 2007) (Fig. 2). The marine transgression is coincidental with the onset of the trace fossil-bearing, shallow-intertidal to supratidal, mainly siliciclastic Tayan Member (up to 21 m thick) of the

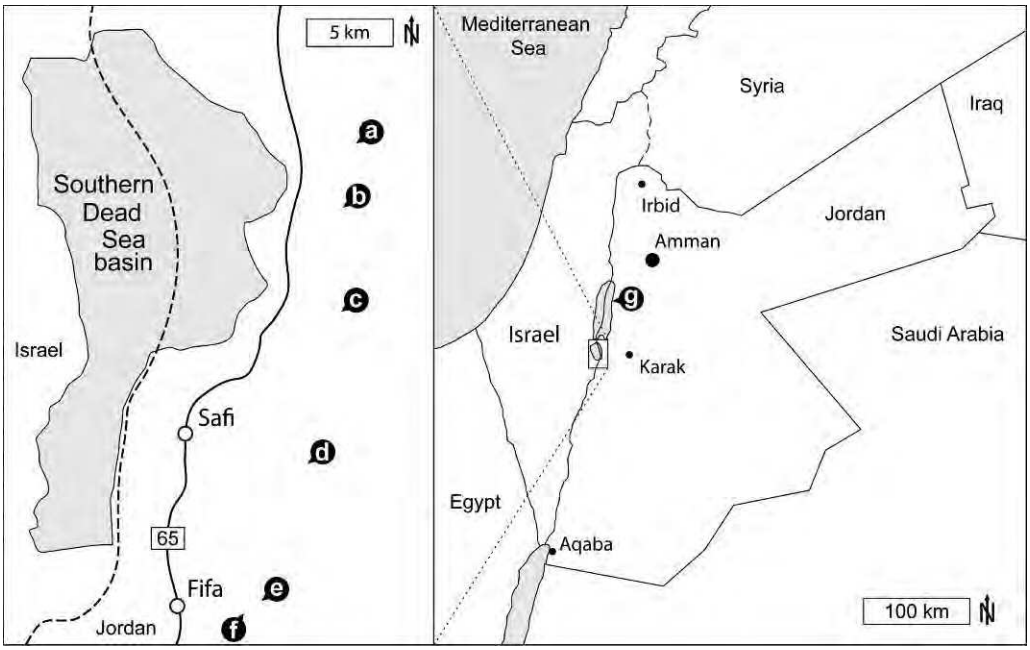

FIGURE 1—Map of Jordan and the Southern Dead Sea area showing the location of all sections mentioned in the *a*, Wadi Issal (N 31°11′21.1″, E 35°33′16.2″); *b*, Wadi Uhaymir (N 31°9′7.0″, E 35°33′45.5″); *c*, Wadi Qunai (N 31°5′48.8″, E 35°33′27.1″); *d*, Wadi Al Hisa (N 31°0′50.2″, E 35°32′20.6″); *e*, Wadi Umm Jafna (N 30°56′23.0", E 35°30′37.7"); *f*, Wadi Fifa (N 30°55′54.00″, E 35°28′42.00″); *g*, Zerqa Ma'in (N 31°37′52.1″, E 35°34′27.9″).

Burj Formation (Elicki, 2007). According to the ichnofauna (simple vermiform trace fossils and *Treptichnus pedum*) and the presence of fossiliferous layers overlying the trace-fossil levels (see below), an "early Cambrian" age for the Tayan Member was proposed (Elicki, 2007). The Numayri Member (up to 61 m thick) is represented by shallow-water, restricted to fully marine, fossiliferous limestone and (mostly diagenetic) dolostone, including a variety of marginal-marine subenvironments, such as lagoons, shoals, intertidal flats and sabkhas (e.g., Shinaq and Bandel, 1992; Rushton and Powell, 1998; Elicki et al., 2002; Shinaq and Elicki, 2007). This member contains trilobites, brachiopods, hyolithids, sponge spicules, and echinoderms, which indicate a stratigraphic position in the traditional lower–middle Cambrian boundary interval (Rushton and Powell, 1998; Geyer and Landing, 2004; Shinaq and Elicki, 2007), equivalent to parts of Stage 5 (Series 3) of the new stratigraphic scheme of the Cambrian system (Elicki, 2011; Elicki and Geyer, in press). The Hanneh Member (up to 35 m thick; Fig. 3) is represented by a transgressive-regressive succession. This shallow-marine succession is exclusively siliciclastic and contains a particularly rich marine ichnofauna (Seilacher, 1970, 1992) and few trilobites (Elicki and Geyer, in press). The return to continental and marginal-marine conditions took place at the base of the overlying siliciclastic Umm Ishrin Formation (Makhlouf and Abed, 1991).

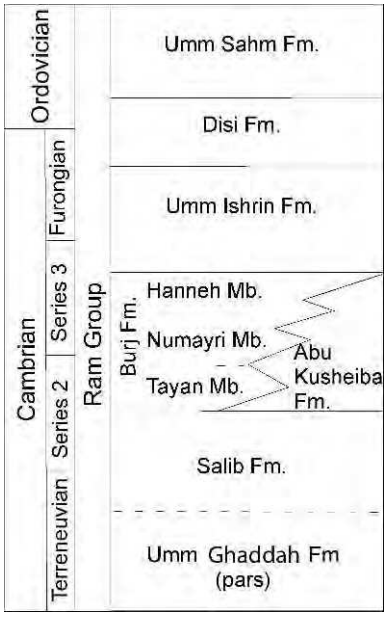

FIGURE 2—Lithostratigraphic scheme of west-central Jordan modified after Rushton and Powell (1998) and Amireh et al. (2008). Fm=Formation; Mb=Member.

The Cambrian marine succession of the southern Dead Sea area was deposited within a shallow-, marginal-marine to continental setting at low paleolatitudes (Elicki et al., 2002). The thickness of the Cambrian succession increases from 0 m north of Aqaba (onlapping the Arabo-Nubian Shield) to around 700 m in the Dead Sea region (Bender, 1974; Powell, 1989). The study area follows the eastern shore of the Dead Sea from the mouth of Wadi Zerqa Ma'in to the area of Ghawr Fifa village immediately south of the Dead Sea (Fig. 1).

SYSTEMATIC ICHNOLOGY

Nineteen ichnogenera and twenty-eight ichnospecies have been identified. Escape trace fossils and undetermined scratch marks were left in open nomenclature. Ichnotaxa are clustered into six informal groups: vertical burrows, horizontal simple burrows and trails, plug-shaped burrows, horizontal branched burrows, bilobate traces, and scratch marks and imprints. Most specimens figured in this paper are housed in the Geological Institute of Freiberg University (Germany) under collection numbers FG 603.

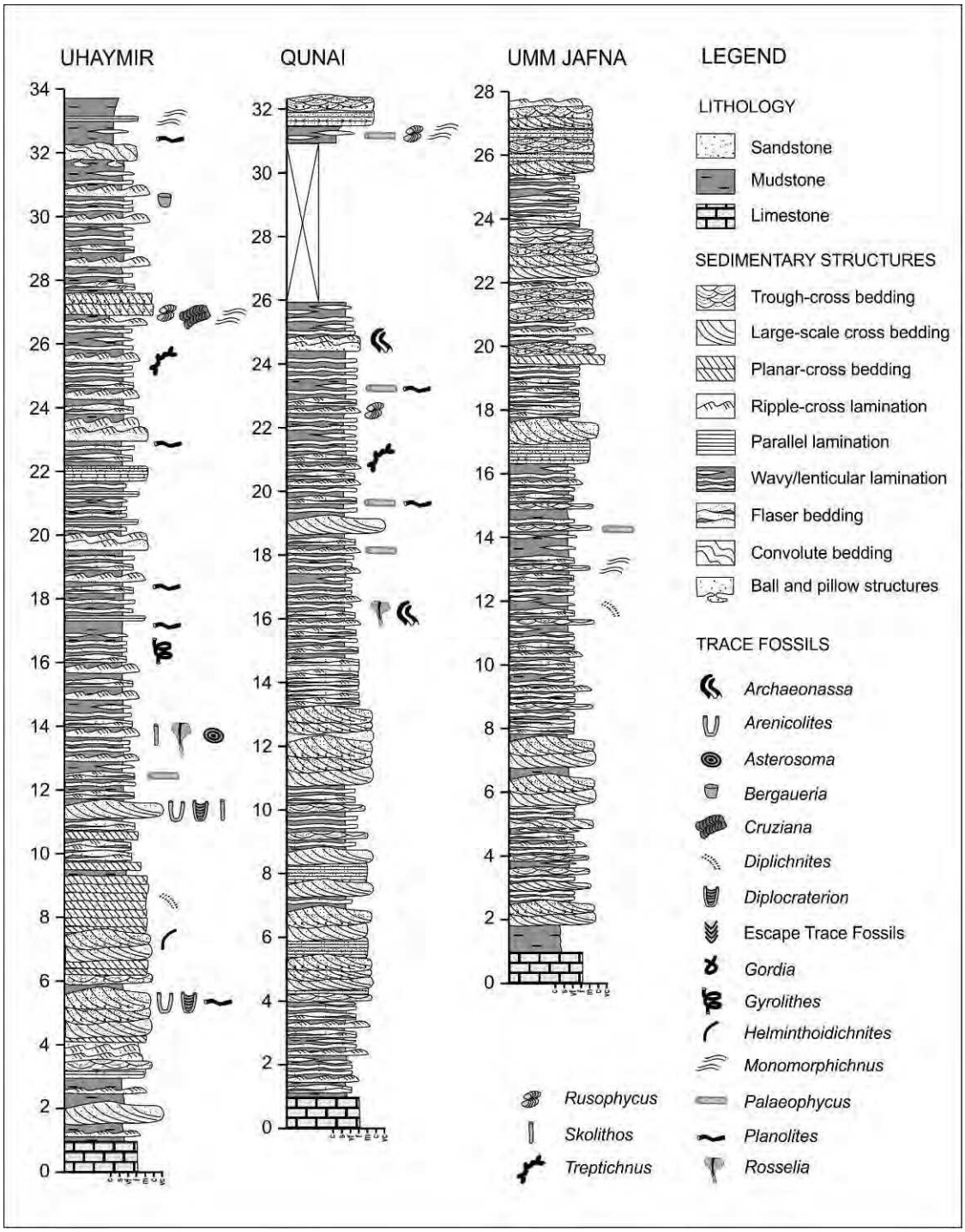

FIGURE 3—Sedimentologic logs of Wadi Uhaymir, Wadi Qunai and Wadi Umm Jafna in the Southern Dead Sea Area showing vertical distribution of the trace fossils.

VERTICAL BURROWS

Ichnogenus ARENICOLITES Salter, 1857
ARENICOLITES isp.
Figure 4.1, 4.2

Specimens.—Several tens of specimens observed in the field, especially common in the lower interval of the Wadi Uhaymir and Wadi Issal sections.

Description.—Vertical U-tubes perpendicular to bedding plane preserved as full relief in cross-sectional views (Fig. 4.2). Locally, paired circular openings visible on the top of bedding planes are suggestive of *Arenicolites*. The burrows are cylindrical, exhibit a massive fill similar to the host sediment. A thin lining might be inferred based on the presence of a sharp contact between infill and host sediment. In many cases, weathering has resulted in the removal of the burrow infill and preservation as

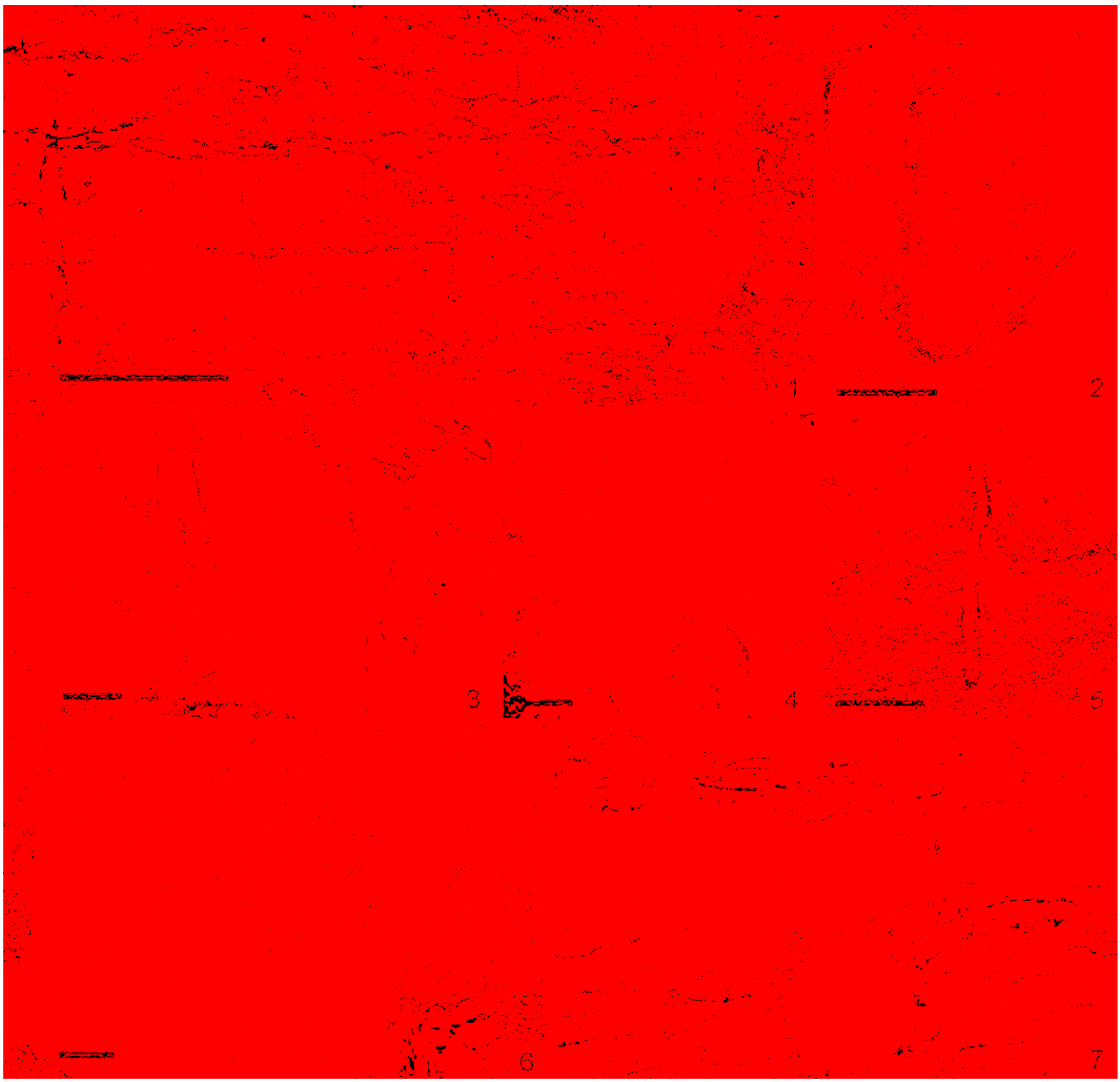

FIGURE 4—Field photographs of vertically oriented burrows. *1,* general view of *Arenicolites* isp. from the sandbar deposits of the Hanneh Member in Wadi Uhaymir, scale=10 cm; *2*, closeup of *Arenicolites* isp. from similar deposits in Wadi Issal, scale=1 cm; *3*, *Diplocraterion* isp. on sandstone top, Hanneh Member, Wadi Uhaymir, scale=2 cm; *4*, *Diplocraterion* isp. on base of sandstone, contact between the Numayri and Hanneh members, Wadi Umm Jafna, scale=1 cm; *5*, *Skolithos linearis* in cross section, Hanneh Member, Wadi Uhaymir, scale=1 cm; *6*, *Skolithos linearis* on sandstone top, Hanneh Member, Wadi Uhaymir, scale=2 cm; *7*, *Gyrolithes polonicus* in full-relief preservation, Hanneh Member, Wadi Uhaymir, coin diameter is 25 mm.

negative epireliefs. Arms are mostly parallel or rarely slightly diverging. Some partially preserved specimens display a J-shaped morphology (Fig. 4.1). Depth is 40 to 75 mm. Arm width is 10 to 18 mm. Burrow diameter is 1 to 2 mm.

Remarks.—*Arenicolites* differs essentially from *Diplocraterion* in the absence of spreiten (Fürsich, 1974a). It is commonly interpreted as a domichnion of suspension-feeding, worm-like organisms (Fürsich, 1974b). However, Bromley (1996) noted that similar structures are produced in modern environments by deposit feeders, including polychaetes, holothurians and enteropneusts. Ichnospecies identification is problematic due to the lack of consistent ichnotaxobases at ichnospecies level and the need for taxonomic revision of the ichnogenus (Mángano et al., 2002).

Ichnogenus DIPLOCRATERION Torell, 1870
DIPLOCRATERION isp.
Figure 4.3, 4.4

Specimens.—Approximately 30 specimens on the base of a slab found in Wadi Uhaymir and partially preserved specimens in

upper bedding plane view in the lower interval of the Wadi Uhaymir section. Additional specimens also occur near the contact between the Tayan Member and the Numayri Member in Wadi Umm Jafna.

Description.—Two main types of preservation have been recorded. Some specimens extend from the bed sole and display the lower bend of the U-tube as positive hyporeliefs (Fig. 4.4). Thickness of burrow is 2 to 3 mm. Width is 7 to 12 mm (dimension terminology following Fürsich 1974b). Burrows are thinly lined, and infill is similar or slightly coarser-grained than host sediment. A second mode of preservation includes dumb-bell-shaped negative epireliefs (Fig. 4.3). In this preservation, burrow thickness is typically 3 mm, and burrow width ranges from 12 to 22 mm.

Remarks.—Although some spreite structures in U-shaped burrows are considered to be an expression of sediment feeding, *Diplocraterion* is convincingly interpreted as a burrow of suspension feeders (Seilacher, 1967; Cornish, 1986; Fürsich 1974b). The spreite in *Diplocraterion* most probably reflect animal growth or adjustment to sedimentation and erosional processes (equilibrichnia of Bromley, 1996). Thus, it can be interpreted as a dwelling tube or an equilibrium structure of a suspension-feeding organism. Bromley (1996), however, noted that *Diplocraterion*-like structures in recent muddy substrates are produced by detritus-feeding amphipods.

Assignment to *Diplocraterion* is based on disturbed sediment between circular openings of the burrow interpreted as the expression of the spreite. Positive hyporelief specimens on slab FG 603 J_02 were cut, revealing that they were passively filled and truncated by the sharp base of the overlying sandstone.

Ichnogenus Gyrolithes De Saporta, 1884
Gyrolithes polonicus (Fedonkin 1981)
Figure 4.7

Specimens.—Six specimens observed in cross sectional view in one bed of the middle interval the Wadi Uhaymir section.

Description.—Vertical spiral structures preserved as full reliefs. Spirals are incomplete and only partial whorls are observed penetrating from the base of a sandstone bed into the underlying green siltstone (Fig. 4.7). Burrow diameter is 3 to 4 mm and typically subcircular to elliptical in cross section. Wall is smooth and the infill consists of light gray fine-grained sandstone contrasting with the greenish ambient siltstone. Maximum depth of penetration is 180 mm. The best preserved specimen is a sinistral spiral burrow with irregular coiling. The incomplete whorl displays an elongate sub-horizontal intersection with a length of 11 mm, indicating a strongly displaced axis. The tunnel diameter shows a slight decrease in size towards the lower end which exhibits a more flattened cross-section.

Remarks.—Seilacher (2007, pl. 33) illustrated a specimen of *Spiroscolex* (=*Gyrolithes*, see Jensen, 1997) from the Cambrian that displays a slightly displaced axis and closely resembles the analyzed material. Based on comparisons with modern examples, Netto et al. (2007) concluded that spiral burrows serve multiple purposes, including dwelling, deposit feeding, anchoring and courtship.

Mesozoic and Cenozoic occurrences are most likely produced by decapod crustaceans (Gernant, 1972; Wetzel et al., 2010). However, other producers (e.g., polychaetes) may have been involved in the lower Paleozoic (e.g., Fillion and Pickerill, 1990; Jensen, 1997). In fact, scratch-mark ornamented walls are absent in lower Paleozoic occurrences. Powell (1977) pointed out that in modern environments some *Gyrolithes*-type burrows are produced by polychaetes.

The related ichnospecies *G. saxonicus* differs from *G. polonicus* in that the former is larger and has a downward expanding spiral (Jensen, 1997). Cambrian spiral burrows are typically referred to *Gyrolithes polonicus*, and are only known from open-marine settings (Netto et al., 2007).

Ichnogenus Rosselia Dahmer, 1937
Rosselia isp.
Figure 5.3–5.5

Specimens.—Fifty specimens observed in the field, being particularly well represented near the top of the lower heterolithic interval in the Wadi Uhaymir, Wadi Issal, and Wadi Qunai sections.

Description.—Vertical to oblique full relief burrows with concentric infill around an off-centered cylindrical shaft (Fig. 5.4, 5.5). These burrows commonly display a pillar-like morphology (Fig. 5.4). Diameter of the burrow slightly and gradually varies along the axis resulting in a faint, bulbous morphology. More rarely, an uppermost funnel-shape or calyx-like structure is visible (Fig. 5.3). On bedding-plane views (Fig. 5.5), cross section is subcircular to slightly elliptical. Burrow length is up to 270 mm but commonly is 100 to 150 mm. Burrow width is 16 to 24 mm. Concentric infill is formed by an alternation of sandstone and mudstone laminae but sandstone laminae tend to be thicker producing a sandstone-dominated infill. The thickness of concentric laminae is 2 to 6 mm, typically increasing from interior to exterior of the structure.

Remarks.—Several workers have compared *Rosselia* with the ichnogenera *Asterosoma* and *Cylindrichnus* (e.g., Chamberlain, 1971; Häntzschel, 1975; Frey and Howard, 1985; Desjardins et al., 2010). Frey and Howard (1985) noted that *Rosselia* has a similar concentric sand-mud infill to that of *Cylindrichnus concentricus*. The latter, however, does not display the funnel-shaped morphology of *Rosselia*. In contrast to *Rosselia*, *Asterosoma* is a branched structure, commonly arranged in flower-shaped patterns with multiple inclined to horizontal components (see Seilacher, 2007, pl. 46). Fillion and Pickerill (1990) regarded ichnogeneric separation as reasonable but they considered *Rosselia*, *Cylindrichnus*, and *Asterosoma* as end members of gradational burrow systems (see also Fürsich, 1974a; McCarthy, 1979).

Rosselia socialis represents a dwelling structure of detritus-feeding organisms and terebellid polychaetes have been suggested as tracemakers in younger examples (Nara, 1995, 2002).

The specimens from the Hanneh Member do not show the typical morphology of *Rosselia socialis* which features a basal stem with a well-developed spindle or onion-shaped top. They resemble pillar-shaped burrows similar to those described as "stacked" variants by Nara (2002, fig. 5b). *Rosselia* from the Hanneh Member also exhibit a sandstone-dominated infill and an off-center inner tube. However, the presence of thin mudstone laminae reveals a concentric infill. Similar specimens of *Rosselia* have been recently described from the lower Cambrian Gog Group of the Canadian Rockies (Desjardins et al., 2010).

Ichnogenus Skolithos Haldemann, 1840
Skolithos linearis (Haldemann, 1840)
Figure 4.5, 4.6

Specimens.—Several tens of specimens observed in Wadi Uhaymir and Wadi Issal.

Description.—Straight to slightly curved, vertical, cylindrical burrow with massive sandstone infill similar to the host rock. Preserved as full relief (Fig. 4.5). A distinct weathered surface in the contact between the sandstone infill and the host rock suggests the presence of an original lining (Fig. 4.5). In bedding-plane preservation, scattered circular openings are recognized (Fig. 4.6). Burrow depth is up to 100 mm and diameter is 2 to 3 mm.

Remarks.—*Monocraterion* differs from *Skolithos* by the presence of a funnel-shaped uppermost top and full-relief tubes

FIGURE 5—Field photographs of concentrically filled burrows, Hanneh Members. *1*, *2, Asterosoma* isp., Wadi Issal, scale=1 cm; *3*, *Rosselia* isp., Wadi Uhaymir, coin diameter is 28 mm; *4*, *Rosselia* isp., Wadi Uhaymir, coin diameter is 25 mm; *5*, *Rosselia* isp. on sandstone top, Qunai, coin diameter is 28 mm.

radiating from the funnel (Alpert, 1974; Jensen, 1997). Jensen (1997) and Schlirf and Uchman (2005) suggested restriction of *Monocraterion* to the type material, a decision which is endorsed by subsequent authors (e.g., Mángano et al., 2005; Desjardins et al., 2010). Furthermore, it has been proposed that a funnel-shaped top is not a suitable ichnotaxobase in simple vertical burrows since it is easily truncated by erosion, and may represent abiotic modification by currents (Fürsich, 1974b). In densely bioturbated beds also containing *Arenicolites* isp., a bedding-plane view does not allow distinction between *Skolithos linearis* and *Arenicolites* isp.

Skolithos is interpreted as a domichnion of suspension feeders or passive predators, including annelids and phoronids (Alpert, 1974; Schlirf and Uchman, 2005).

Escape Trace Fossils
Figure 6.1, 6.2

Specimens.—Five specimens observed near the top of the Wadi Uhaymir section.

Description.—Funnel-shaped vertical to steeply inclined structures formed by a series of nested inverted cones. Most structures are slightly to very asymmetrical in morphology. Structures are 7 to 9 mm wide and 12 to 22 mm long, with the lower end of the structure typically pointed. The upper end of the structure may be represented by a concave, depressed area (Fig. 6.1), or is almost indistinct, with lateral laminations opening upward into the overlying sandstone (Fig. 6.2).

Remarks.—Conical structures crossing laminated or cross-bedded sandstone are traditionally divided into two groups according to their origin: escape or interrupted animal upward movement in relation to an increasing or punctuated sedimentation rate, and liquid or gas escape structures of inorganic origin. Buck and Goldring (2003) provided a detailed analysis of criteria

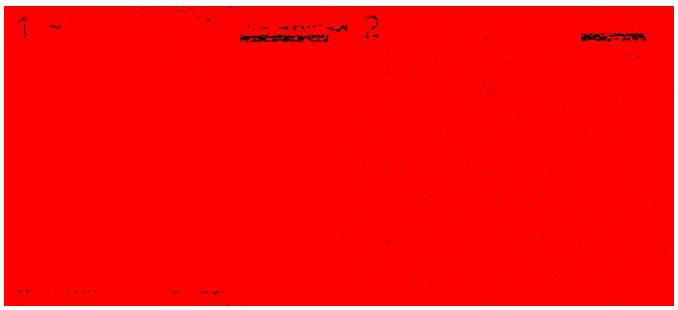

FIGURE 6—Escape trace fossils, transition between the Hanneh Member and the Umm Ishrin Formation, Wadi Uhaymir. *1*, field photograph, V-shaped burrow in parallel-laminated, fine-grained sandstone (lower left), scale=2 cm; *2*, closeup of polished slab (FG 603 T_07) showing slightly asymmetrical V-shaped, escape structure, scale=1 cm.

to understand the processes involved in the generation of conical structures of biogenic origin. In particular, structures displaying step-like lamina displacements defining a series of arcuate shear planes propagating from a lower point are attributed to collapse structures. Morphologic analysis of the funnel-like structures indicates collapse structures in loosely packed sands associated with a small lower cavity generated by the rapid upward movements of a small animal (Buck and Goldring, 2003). Rapid upward locomotion produced downward advection and deformation of the loose sediment. The fact that the animal was small sized (and only a small lower cavity was created) resulted in a relatively narrow deformation zone, V-shaped downwarping of sediment laminae and a shallow, concave surface depression (Buck and Goldring, 2003, fig. 3). The upward decrease in deformation is also indicative of a small or deeply buried structure in which the volume change is completely compensated by passive infilling within sediment body.

Horizontal Simple Burrows and Trails

Ichnogenus Archaeonassa Fenton and Fenton, 1937
Archaeonassa fossulata (Fenton and Fenton, 1937)
Figure 7.1

Specimens.—Fifteen specimens examined in the field in Wadi Qunai and Wadi Uhaymir.

Description.—Narrow, concave axial grooves locally flanked by marginal positive ridges preserved as epireliefs. Course is curved, irregularly winding, rarely meandering or subcircular (Fig. 7.1). Overcrossing among specimens is common, self-overcrossing is rarely present. Axial groove is 1 to 2 mm wide. Some specimens display very incipient flanking structures but others exhibit well-developed, slightly flat, positive ridges. Width is 2 to 5 mm but typically is around 2.5 mm.

Remarks.—*Archaeonassa* has been extensively used for simple trails displaying a median groove flanked by levees (e.g., Buatois and Mángano, 2002; Jensen, 2003; Jensen et al., 2006). Early interpretations on the producer of *Archaeonassa* included gastropods (Fenton and Fenton, 1937). Buckman (1994) endorsed production by gastropods but also suggested echinoids and trilobites. In contrast, Yochelson and Fedonkin (1997) excluded gastropods due to their inferred inability to burrow and proposed instead "arthropods of some sort." *Archaeonassa*, however, does not display any scratch mark ornamentation or any morphologic detail that suggests appendages as burrowing tools. Jensen (2003) inferred that Ediacaran and lower Paleozoic *Archaeonassa* might have been created by "mollusc-type" animals as indicated by the characteristically central flat area between the ridges.

The specimens studied form dense monospecific assemblages preserved at the interface between ripple cross-laminated, fine-grained sandstone and a thin mudstone drape. Distinction from *Helminthopsis* and *Helminthoidichnites* may be problematic in epichnial preservation. In particular, some specimens of *Archaeonassa* are gradational with these ichnotaxa (Fig. 7.1). The possibility that negative epireliefs assigned to *Helminthopsis* and *Helminthoidichnites* record poorly preserved specimens of *Archaeonassa fossulata* cannot be ruled out. None of the specimens analyzed display a median flat zone suggestive of true epifaunal plowing. Accordingly, the producer is thought to have moved through the sediment, immediately beneath the sediment-water interface (Jensen, 2003).

Ichnogenus Gordia Emmons, 1844
Gordia marina (Emmons, 1844)
Figure 7.2, 7.3

Specimens.—Approximately 30 specimens examined in the field in Wadi Uhaymir, Wadi Umm Jafna, and Wadi Issal.

Description.—Smooth specimens either preserved as negative epireliefs (Fig. 7.2) or as positive hyporeliefs (Fig. 7.3). Course is winding and typically looping with self-crossings. Width is 1 to 3 mm but is typically 1 to 2 mm. Width is approximately uniform along individual specimens. In hypichnial preservation (Fig. 7.2), burrow infill is massive and similar to the host rock.

Remarks.—*Gordia* is characterized by self overcrossing (e.g., Buatois et al., 1998; Gaigalas and Uchman, 2004; Lerner et al., 2007). A similar ichnogenus is *Mermia* which was recently regarded as a junior synonym of *Gordia* (Uchman et al., 2009). However, *Mermia* displays strong, consistent looping (Walker, 1985) revealing less specialized feeding behavior, and should be regarded as a different ichnogenus. *Gordia* is interpreted as a grazing trail or pascichnion of numerous organisms, including arthropods, polychaete annelids (Pickerill et al., 1987), and molluscs (Gaigalas and Uchman, 2004). Specimens preserved as epireliefs may intergrade with *Archaeonassa* and *Helminthoidichnites*.

Ichnogenus Helminthoidichnites Fitch, 1850
Helminthoidichnites tenuis (Fitch, 1850)
Figure 7.4

Specimens.—Approximately 20 specimens observed in Wadi Issal and Wadi Uhaymir.

Description.—Thin, smooth burrows or trails predominantly preserved as positive hyporelief. Course is straight to gently curved or circular (Fig. 7.4). Width is 0.5 to 2.0 mm. Fill is massive. Trails do not self-overcross but overlap among specimens is common.

Remarks.—*Helminthoidichnites* was regarded as a junior synonym of *Gordia* by Häntzschel (1975). However, subsequent studies (e.g., Buatois et al., 1998; Gaigalas and Uchman, 2004) retained this ichnogenus and morphometric analysis (Hofmann, 1990) has confirmed the validity of *Helminthoidichnites*. Marine occurrences of *Helminthoidichnites* are generally referred to worm-like organisms (Hofmann and Patel, 1989). This ichnogenus is interpreted as a non-specialized grazing trail (Buatois et al., 1997). Some of the Hanneh specimens show intergradations with *Gordia*, indicating a common producer.

Ichnogenus Palaeophycus Hall, 1847
Palaeophycus tubularis (Hall, 1847)
Figure 7.5, 7.6

Specimens.—Approximately 60 specimens observed in the field and an additional twenty specimens recorded on slabs from Wadi Issal, Wadi Uhaymir, Zerqa Ma'in, Wadi Qunai, and Wadi Umm Jafna.

Description.—Straight to curved, horizontal to slightly inclined, thinly lined cylindrical burrows, preserved as full reliefs (Fig. 7.5). The boundary of the structure is generally smooth or irregularly wrinkled in few specimens. Fill is massive and identical to host sediment. False branching due to overlap of specimens is common on crowded bedding planes (Fig. 7.6). Width is 1 to 9 mm but most commonly 4 to 7 mm.

Remarks.—The most accepted ichnotaxonomic scheme for *Palaeophycus* is that of Pemberton and Frey (1982). They recommended assigning actively filled unlined burrows to *Planolites* and passively filled burrows to *Palaeophycus*. However, Jensen (1997) noted that digested material may resemble the host sediment and passively introduced sediment may contrast with the host sediment. Accordingly, rather than the nature of the infill (contrasting vs. similar to the host rock), analysis of whether the structure records active reworking by the producer or simple passive downward advection is required to produce a sound classification. *Palaeophycus* is interpreted as a dwelling burrow of suspension-feeding or predator worms (Pemberton and Frey, 1982). *Palaeophycus tubularis* is distinguished from other ichnospecies of *Palaeophycus* by a thin lining

FIGURE 7—Field photographs of horizontal burrows and trails, Hanneh Member. *1*, *Archaeonassa fossulata*, Wadi Umm Jafna, coin diameter is 28 mm; *2*, *Gordia marina,* Wadi Umm Jafna, coin diameter is 23 mm; *3*, *Gordia marina,* Wadi Issal; *4*, *Helminthoidichnites tenuis* seen in positive hyporelief on float from section Wadi Uhaymir; *5*, *Palaeophycus tubularis,* Zerqa Ma'in; *6*, *Palaeophycus tubularis*, Wadi Qunai, slab FG 603 Q_04; *7*, *Planolites beverleyensis*, Wadi Issal; *8*, *Planolites montanus,* Wadi Issal; *9*, *Planolites montanus* in cross-section view, Wadi Issal. All scale bars=1 cm.

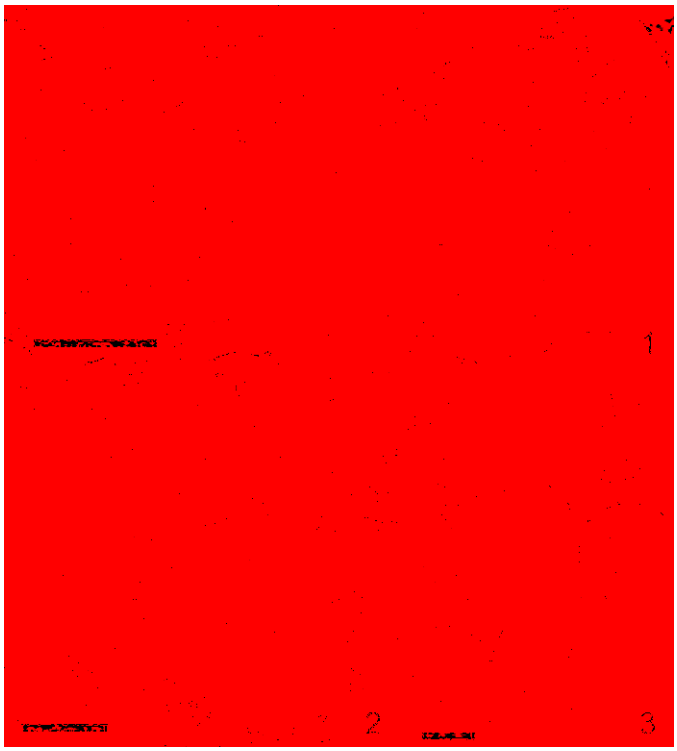

FIGURE 8—Field photographs of the base of a sandstone bed containing *Bergaueria sucta*, Hanneh member, Wadi Uhaymir. *1*, general view, scale=5 cm; *2*, closeup of *Bergaueria sucta* showing lateral displacement pattern, scale=2 cm; *3*, same as in 2, scale=1 cm.

and the absence of striations. However, contorted or wrinkled walls may result from compaction of open burrows.

Ichnogenus PLANOLITES Nicholson, 1873

Remarks.—*Planolites* represents the work of vagile infaunal deposit-feeding vermiform organisms (Pemberton and Frey, 1982).

PLANOLITES BEVERLEYENSIS (Billings, 1862)
Figure 7.7

Specimens.—Approximately 15 specimens on slab FG 603 J_01 found as float in Wadi Umm Jafna and dozen of specimens observed in the field in Wadi Issal.

Description.—Subcylindrical to cylindrical, horizontal vermiform structures with irregularly constricted surface, predominantly preserved as positive epirelief and hyporelief (Fig. 7.7). Width is 1 to 4 mm. Course is irregular, gently curved, or arcuate. Overlap among specimens is common. Fill is coarser-grained than the host rock.

Remarks.—The constrictions clearly point to an active infill. Deposit feeding was mostly constrained to an interfacial sand-mud boundary. *Planolites beverleyensis* differs from *Planolites montanus* in its curved to arcuate courses and more penetrative nature (Pemberton and Frey, 1982).

PLANOLITES MONTANUS (Richter, 1937)
Figure 7.8, 7.9

Specimens.—Hundreds of specimens observed in the field in all analyzed sections.

Description.—Subcylindrical to cylindrical, horizontal to inclined vermiform structures with smooth surface, predominantly preserved as full-reliefs within heterolithic facies (Fig. 7.8). Burrow width is 1 to 8 mm but is most commonly 3 to 5 mm. Overlap among specimens is common. Fill differs from hostrock in being typically finer-grained.

Remarks.—*Planolites montanus* is distinguished from other ichnospecies of *Planolites* by its tortuous course with horizontal and inclined segments, penetrative nature, and lack of ornamentation (Pemberton and Frey, 1982).

PLUG-SHAPED BURROWS

ICHNOGENUS BERGAUERIA Prantl, 1946
BERGAUERIA SUCTA (Seilacher, 1990)
Figure 8.1–8.3

Specimens.—Four specimens collected (slabs FG 603 F_01, FG 603 T_07, FG 603 T_10) in addition to more than 20 specimens observed in the field in Wadi Uhaymir.

Description.—Circular disc-shaped structures, displaying a laterally repeated pattern of crescent-shaped impressions (Fig. 8.2). Preserved as positive hyporeliefs. Successive lateral positions are recorded by a series of five to ten impressions showing lateral displacement in one direction (Fig. 8.3). Disc-shaped impressions are commonly slightly inclined in relation to the bedding plane. Diameter of impressions is 14 to 44 mm. Specimens rarely occur as single disc-shaped impressions without lateral crescentic pattern. Spiraling radial markings (see Seilacher, 1990, p. 666) are not clearly discernible.

Remarks.—Pemberton et al. (1988) considered four *Bergaueria* ichnospecies as valid (*B. perata, B. langi, B. radiata,* and *B. hemispherica*). A fifth ichnospecies, *Bergaueria sucta*, was erected by Seilacher (1990). *Bergaueria sucta* is remarkably different from the other ichnospecies included in *Bergaueria*. While all ichnospecies of *Bergaueria* are single-entrance burrows with a more or less plug-shaped morphology, *B. sucta* exhibits a particularly flat discoidal morphology.

Bergaueria is interpreted as a domichnion or cubichnion produced by actinarian and ceriantharian coelenterates (e.g., Fillion and Pickerill, 1990; Pemberton et al., 1988; Bromley, 1996).

Seilacher (1990) defined *B. sucta* based on specimens from the lower Cambrian Mickwitzia Sandstone of Sweden that he interpreted as impressions of a flat, disc-shaped base of actinian cnidarians. The laterally repetitive crescentic pattern records the sideway-migration of the tracemaker. Some of the Hanneh specimens are similar to material described by Jensen (1997, p. 99, fig. 66) as "arcuate burrows."

HORIZONTAL BRANCHED BURROWS

IchnogenusASTEROSOMA von Otto, 1854
ASTEROSOMA isp.
Figure 5.1, 5.2

Specimens.—Twelve specimens observed in a small cliff in the upper part of Wadi Issal.

Description.—Full relief horizontal to inclined inflated burrows with concentric layers around a central cylindrical shaft (Fig. 5.2) and radiating from a central point. The concentric infill typically consists of alternating claystone and sandstone layers (Fig. 5.1). Diameter of central shaft is 1 to 5 mm. Width of overall burrow is 4 to 13 mm.

Remarks.—*Asterosoma* is a feeding structure suggested to have been produced by vermiform organisms (Chamberlain, 1971) or crustaceans (Müller, 1971; Neto de Carvalho and Rodriguez, 2007). Striae are interpreted by Seilacher (2007) as microfault patterns caused by animal activity, in particular packing and radial outward pushing of the infill.

The naturally polished surface that host the *Asterosoma* isp. specimens in Wadi Issal exhibits a preservation quite similar to that observed in cores. The gross overall morphology of the studied specimens is unknown, but the presence of clusters of

FIGURE 9—Field photographs of horizontal trails and burrows, Hanneh Member. *1*, *Cruziana salomonis* and *Phycodes* isp. as positive hyporelief, Zerqa Ma'in, scale=1 cm; *2*, *Treptichnus* cf. *pedum* as positive hyporelief, float, Wadi Uhaymir, scale=1 cm.

concentrically filled burrows radiating from a central point supports assignment to *Asterosoma*. The presence of retrusive spreite suggests adjustment after sedimentation events. Similar trace fossils are figured by Seilacher (2007, pl. 46) as "asterosomid" burrows. Due to the limited knowledge of the 3-D morphology of these structures, classification at ichnospecies level is not possible.

Ichnogenus PHYCODES Richter, 1850

PHYCODES isp.

Figure 9.1

Specimens.—Three specimens observed in Zerqa Ma'in.

Description.—Bundle consisting of five to eight subparallel, cylindrical burrows preserved as positive hyporelief. Individual burrows segments are horizontal or slightly oblique to bedding plane (Fig. 9.1). Diameter of individual segments is 4 to 8 mm. The length of tubes varies within specimens, and is up to 70 mm. Diameter of individual probes remains relatively constant within a single specimen. Width of overall structure is 20 to 60 mm. Fill is massive and slightly finer-grained than the host rock.

Remarks.—*Phycodes* is widely used for horizontal, bundled burrow systems showing a broomlike or flabellate overall morphology (Han and Pickerill, 1994; Seilacher, 2007). It is interpreted as a fodinichnion of annelids (Osgood, 1970; Seilacher, 2000).

The material from the Hanneh Member resembles the Lower Ordovician *P. parallelum* in the presence of a cluster of subparallel probes (Seilacher, 2000). However, the rather indistinct form and non-recurrent bundle pattern prevent identification at ichnospecies level.

Ichnogenus TREPTICHNUS Miller, 1889

TREPTICHNUS cf. T. PEDUM (Seilacher, 1955)

Figure 9.2

Specimens.—Two specimens found as float on hill slope in Wadi Uhaymir and Wadi Umm Jafna.

Description.—Burrow systems consisting of four individual elongate, straight to slightly curved smooth segments, preserved as positive hyporeliefs (Fig 9.2). Segments follow a straight to slightly curved course, individual segments being slightly displaced in relation to each other. Segments are either simple or spindle shaped. Length of individual segments is 7 to 10 mm and width is 2 to 3 mm. Length of structure is about 40 mm. Fill is massive and similar to the host rock.

Remarks.—*Treptichnus* is interpreted as a fodinichnion made by vermiform animals (Buatois et al., 1998). Recent neoichnologic work has convincingly argued for a priapulid origin for *Treptichnus pedum* (Vannier et al., 2010).

Originally described as *Phycodes pedum* (Seilacher, 1955), Jensen (1997) referred this ichnospecies to *Treptichnus* whereas Geyer and Uchman (1995) placed it in *Trichophycus*. The type specimen (Seilacher, 1955, p. 387, fig. 4a) shows branching at the end of the burrow system resulting in a sickle-shaped appearance. Jensen (1997) included more irregular branching patterns with curved to highly winded courses and alternating or single sided segments. The proposal by Jensen (1997) became generally accepted (e.g., Seilacher et al., 2005; Seilacher, 2007; Vannier et al., 2010). Although the scarcity and incomplete nature of the Hanneh specimens prevent from a definite assignment, the overall morphology corresponds with descriptions by Jensen (1997).

BILOBATE TRACE FOSSILS

Ichnogenus CRUZIANA d'Orbigny, 1882

Remarks.—Although commonly regarded as a locomotion trace, *Cruziana* has been interpreted by several authors (e.g., Bergström, 1976; Jensen, 1997; Schmalfuss, 1981; Seilacher, 1985; Mángano et al., 2002; Brandt, 2008) as related to feeding activities. Bergström (1976) pointed out that several *Cruziana* are too deep or required too much energy to represent an expression of pure locomotion behavior. The most significant morphologic feature of *Cruziana*, the bilobate furrows with transverse to V-shaped striae, can be explained by assuming a combined locomotion and feeding strategy (i.e., pascichnion). The reconstructed locomotion can be characterized as a metachronal wave

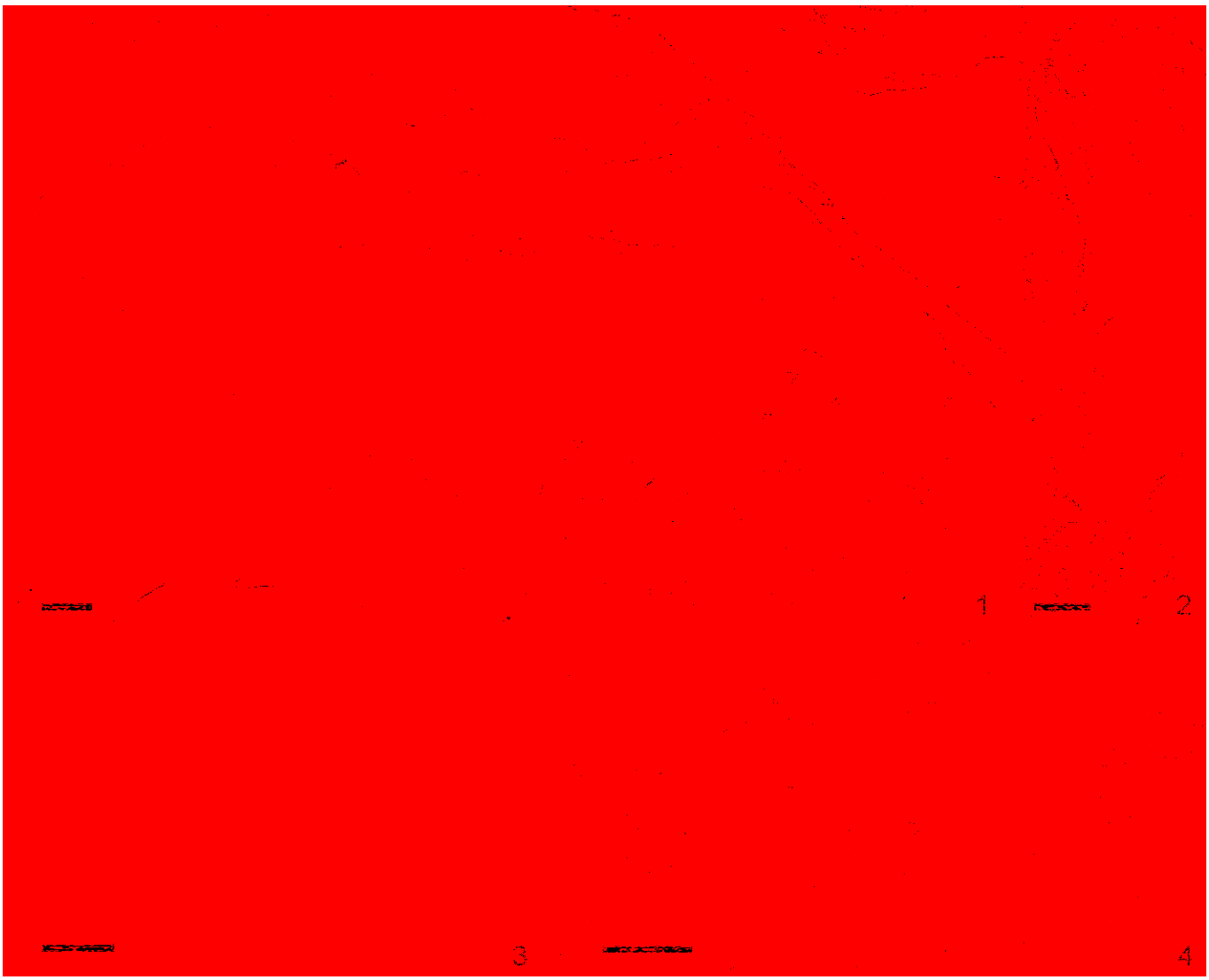

FIGURE *10*—Base of sandstone block containing *Cruziana jordanica* and *Rusophycus aegypticus,* Hanneh Member, Wadi Umm Jafna, FG 603 J_03. *1*, oriented intergrading *Rusophycus aegypticus* and *Cruziana jordanica*, scale=2 cm; *2*, successive *Rusophycus aegypticus*, scale=2 cm; *3*, *Rusophycus aegypticus*, scale=1 cm; *4*, *Cruziana jordanica*, scale=2 cm.

motion from posterior to anterior with an individual medio-posterior leg stroke (Crimes, 1975; Seilacher, 1985). In the course of the leg movement, food particles are moved towards the axis and are being forwarded to the mouth through the coxal groove. Furthermore, circling and scribble-like patterns in *Cruziana semiplicata* and *Cruziana rugosa* suggest a poorly specialized pascichnial pattern (Seilacher, 1970; Neto de Carvalho, 2006).

It is widely accepted that the main producers of *Cruziana* and *Rusophycus* in the early and middle Paleozoic were trilobites or trilobitomorphs. Nevertheless, numerous other arthropods may have been able to produce *Cruziana* (Donovan, 2010; Schatz et al., 2011). In particular, small ichnospecies (e.g., *C. problematica*) that lack significant morphologic criteria are common in continental settings and post-Paleozoic strata, clearly indicating non-trilobite producers (e.g., Bromley and Asgaard, 1972; Schlirf et al., 2001).

CRUZIANA JORDANICA n. isp.
Figure 10.1, 10.2, 10.4

Specimens.—One specimen on slab FG 603 Q_05, 5 specimens on a block from Wadi Umm Jafna and several tens of specimens observed in the field at Wadi Umm Jafna and Wadi Qunai.

Type.—Holotype, specimen in the field but latex cast deposited in collection (FG 603 J_03), Wadi Umm Jafna (Fig. 10.4).

Etymology.—Referring to Jordan, its country of origin.

Diagnosis.—Flat, small *Cruziana* with endopodal scratches arranged in an obtuse V-pattern (V-angle 100° to 160°). Smooth outer lobes may be present.

Description.—Flat, bilobate trails preserved as shallow positive hyporeliefs. Width is 20 to 25 mm. Median axis is typically poorly developed. Smooth, relatively narrow (up to 4 mm wide) outer lobes may be present. Inner lobes are prominent, covered by faint to relatively distinct striae (Fig. 10.4). Sets of V-angle, endopodal scratch marks may vary along the structure, 100° to 160°, generating an undulating fashion. Along the trail, ribbon-like segments alternate with segments composed of aligned rusophycid-like structures (Fig. 10.1), or terminate in a well-defined *Rusophycus* (Fig. 10.2).

Remarks.—Seilacher (1990) proposed the name *Cruziana aegyptica* for "rusophycid expressions" of *Cruziana*. Since the separation of *Cruziana* and *Rusophycus* is favored in this study,

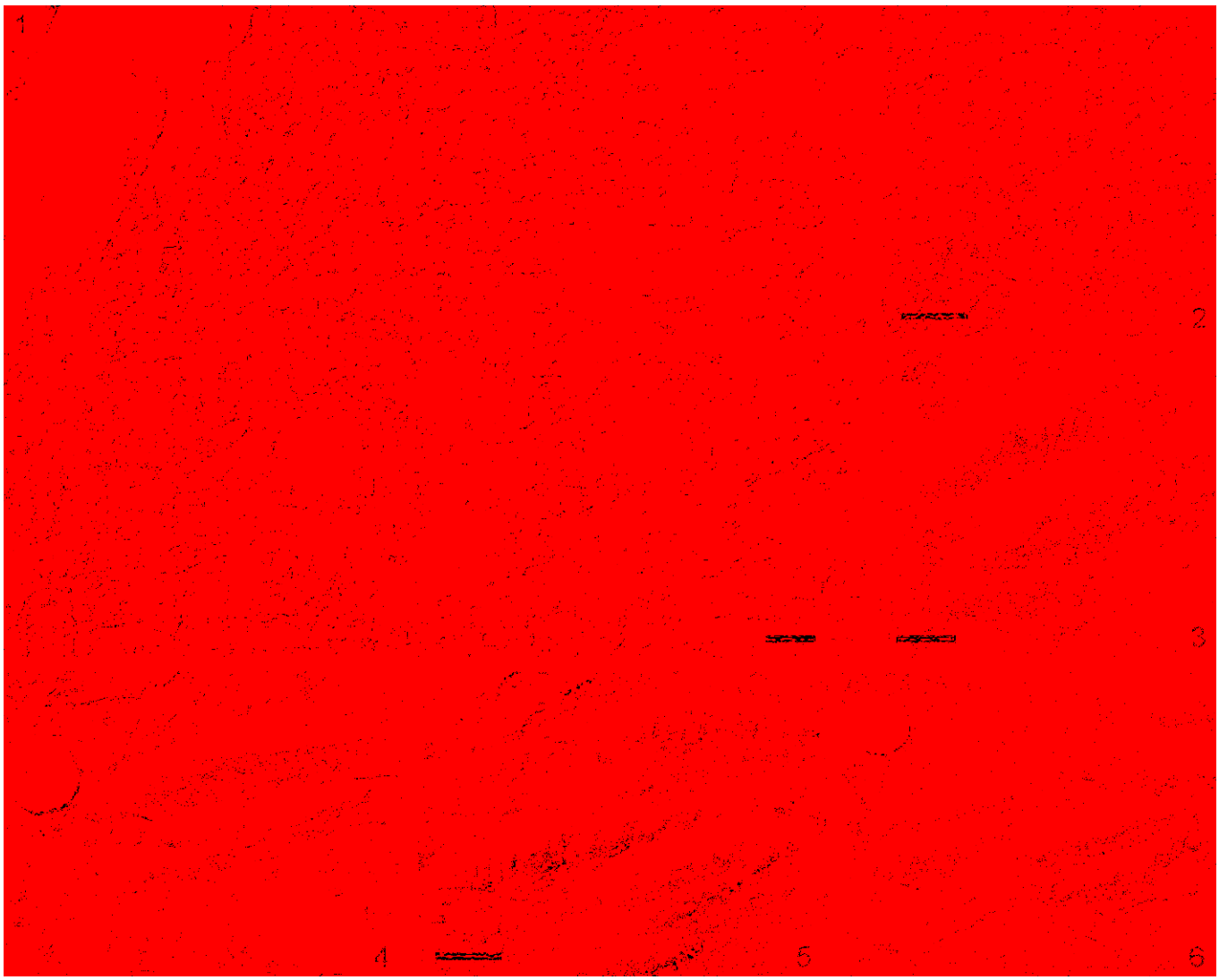

FIGURE *11*—Bilobate structures on the base of a sandstone block, Hanneh Member, Wadi Al Hisa. *1*, general view of surface with *Cruziana problematica* and *Rusophycus carbonarius*, scale=10 cm; *2*, detailed view of loops and loosly meandering *Cruziana problematica*, small coffeebean-shaped impression are *Rusophycus carbonarius,* scale=4 cm; *3*, closeup of *Rusophycus* isp., scale=2 cm; *4*, closeup of *Rusophycus* isp., note associated smaller bilobate trails, coin diameter is 28 mm; *5*, same as in 4; scale=2 cm; *6*, general view of several specimens of *Rusophycus* isp., coin diameter is 28 mm.

those specimens have been relocated in *Rusophycus aegypticus* (see below). The ichnospecies *C. jordanica* is herein introduced for trails or cruzianiform specimens displaying similar scratch pattern to or interconnected with *Rusophycus aegypticus*. Although several specimens of the Hanneh Member can be clearly regarded as continuous plow marks and are herein considered trails best included in *Cruziana*. Additionally, the morphology of *C. jordanica* is distinctive from its rusophycid counterpart. *Cruziana jordanica* is characterized by high angle to transversal endopodal marks and absence of (or rarely very thin) exopodal lobes suggesting a strong prosocline burrowing attitude. *Cruziana jordanica* is commonly intergradational with *R. aegypticus* indicating the same producer for both structures. The local presence of a thin exopodal lobe and the change in the angle of endopodal scratches along the structure differentiates *C. jordanica* from *C. problematica*. *Cruziana jordanica* diplays neither the well-developed exopodal lobes nor the trifid endopodal scratch marks of the well-established upper Cambrian to Lower Ordovician *Cruziana semiplicata* (Seilacher, 1970, 1990).

CRUZIANA PROBLEMATICA (Schindewolf, 1928)
Figure 11.1, 11.2

Specimens.—Several tens of specimens on one block from Wadi Al Hisa and in various intervals in Wadi Umm Jafna in both the Hanneh Member and in the overlying Umm Ishrin Formation.

Description.—Small strongly convex bilobate trails preserved as positive hyporeliefs. Oblique to transversal striae within the lobes are rarely present. Length is highly variable and is 2 to 12 cm. Width is typically 8 to 12 mm. A few specimens exhibit a faint longitudinal ridge approximately in the middle of each individual lobe. Their course varies from straight, curving to irregular meandering (Fig. 11.1). Many specimens tend to form loops (Fig. 11.2). Self-overcrossing is not observed. Overlap among specimens is common.

Remarks.—Jensen (1997) regarded *Cruziana problematica* as a junior synonym of *Cruziana tenella*. However, *Cruziana problematica* is widely reported and is considered the more stable ichnospecies (e.g., Mángano et al., 2002). Some specimens of *Cruziana problematica* show faint oblique scratch marks which

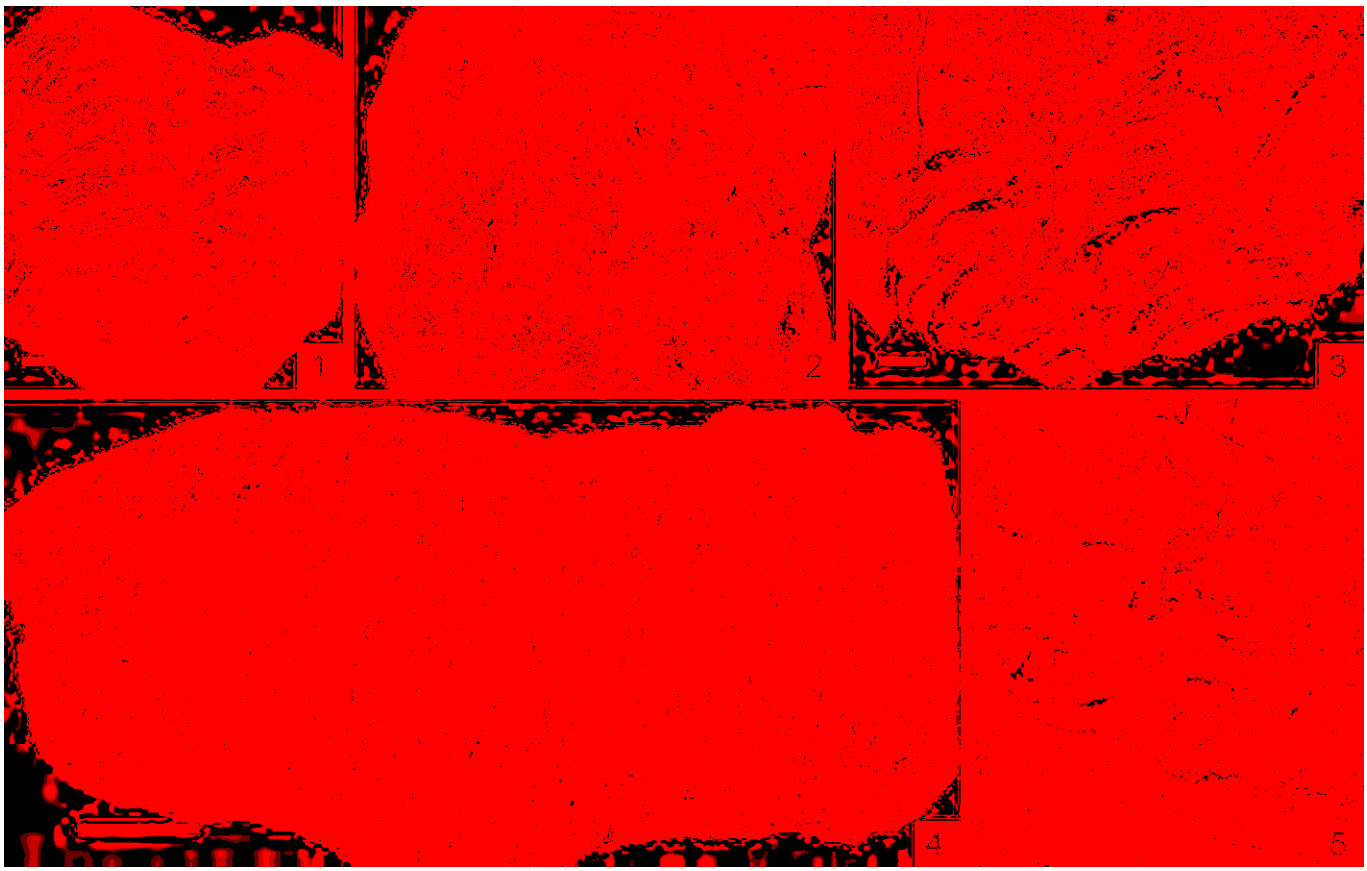

FIGURE *12*—Bilobate structures, Hanneh Member. *1*, *Rusophycus burjensis* n. isp., Zerqa Ma'in, holotype, FG 603 Z_01; *2*, *Cruziana salomonis*, FG 603 T_08; *3*, *Rusophycus burjensis* n. isp., Wadi Qunai, FG 603 Q_03; *4*, *Cruziana salomonis*, Wadi Uhaymir, FG 603 T_13; *5*, *Rusophycus burjensis* n. isp., Wadi Qunai, FG 603 F_01. All scale bars=1 cm.

emerge from the median furrow and disappear within the lobes. Schlirf et al. (2001) considered this feature diagnostic for *Cruziana problematica*. However, we suggest that such structures may be easily subjected to preservational bias. The local presence of longitudinal ridges internal to the lobe (contrasting to marginal ridges) may suggest a rather indistinct differentiation of endopodal and exopodal lobes. This ichnospecies is in need of taxonomic re-evaluation (see Schatz et al., 2011). The Jordan specimens show a tendency to meandering or to form irregular loops and are herein interpreted as combined locomotion and feeding trails (i.e., pascichnia).

CRUZIANA SALOMONIS (Seilacher, 1990)
Figures 9.1, 12.2, 12.4

Specimens.—Approximately 15 specimens observed in Zerqa Ma'in, and four additional specimens on slabs from Wadi Uhaymir (FG 603 T_13) and Wadi Issal (FG 603 I_01). At least five additional specimens found as float in Wadi Issal.

Diagnosis.—Emended: rather large, convex *Cruziana* with one larger and up to four, but typically two or three, slightly smaller, secondary claw marks. Scratch marks are typically bundled in groups of three or four, running subparallel to each other, and transversal to the median axis (Fig. 12.2, 12.4). Exopodite brushings commonly absent (modified from Seilacher, 1990).

Description.—Medium- to large-sized, strongly convex bilobate structures with well-developed endopodal scratch marks preserved as positive hyporeliefs. Width is 40 to 70 mm. Length is 70 to 140 mm. Depth is 5 to 20 mm. Scratch marks are prominent, straight to slightly curved, and occur in sets of up to four main parallel ridges, although typically three are clearly observed. Scratch marks are commonly perpendicular to trace axis recorded as a medial irregular depression. Exopodal scratch marks are absent.

Remarks.—Seilacher (1990) erected *Cruziana salomonis* based on material from the Dead Sea (Zerqa Ma'in) and Sinai, and included both cruzianiform and rusophyciform expressions. Both forms are herein considered as distinct ichnotaxa. Seilacher (1990) included *C. salomonis* in the *barbata* group since they share common features, such as 1) prosocline burrowing technique; 2) diagnostic claw formula involving one or two main claws and up to four secondary claws; and 3) functional differentiation of anterior and posterior endopodites. However, Seilacher (1992) included both *C. barbata* and *C. salomonis* within the *dispar* group, essentially based on a similar claw formula and rusophycid expressions displaying proverse (anterior) and retroverse (posterior) diggings.

Cruziana salomonis is morphologically close to *Cruziana irregularis* (the cruzianiform expression of *R. dispar*, see Jensen 1997) from the lower Cambrian of Poland and Sweeden (Orłowski, 1992; Jensen, 1997). However, *Cruziana salomonis* tends to form deeper plows with a narrower axial zone. In addition, scratch mark groupings, in particular the multiple secondary claw marks, are far more distinct than in *C. rusoformis* (Jensen, 1997). Also, the associated rusophycid expressions, *R. burjensis* and *R. dispar*, display significant morphologic differences reflecting dissimilar burrowing behavior and paleobiologic affinity (see *R. burjensis*). *Cruziana warrisi* from the lower Cambrian of New South Wales displays multiple, subequal, thinner scratch marks (Webby, 1983). *Cruziana omanica* from the

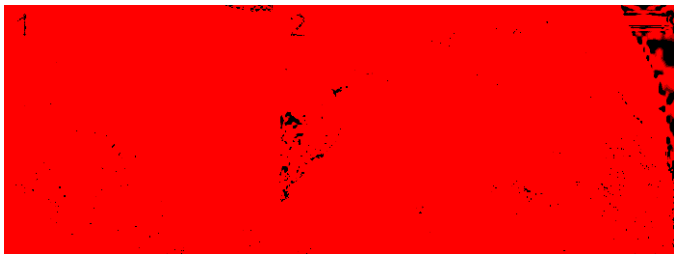

FIGURE 13—*Rusophycus* cf. *R. leifeirikssoni*, Wadi Uhaymir, FG 603 T_06: *1*, ventral view; *2*, lateral view. All scale bars=1 cm.

Cambrian–Ordovician of Oman displays only trifid (commonly bifid), rounded scratch marks, and is associated with highly convex, transverse *Rusophycus latus* (Mángano et al., 1996). *Cruziana salomonis* is commonly associated with *Rusophycus burjensis* suggesting a common tracemaker. As originally stated by Seilacher (1990), *C. salomonis* is best attributed to the activities of medium to large trilobites mostly digging within sand. *Cruziana salomonis* is a poorly known ichnotaxon. An incomplete specimen from the lower Cambrian of Turkey was assigned to *Cruziana* ?*salomonis* by Erdoğan et al. (2004).

Ichnogenus RUSOPHYCUS Hall, 1852

Remarks.—Classical interpretations considered *Rusophycus* as a simple resting structure. However, this ichnotaxon can be quite complex in morphology and has been related to a wide variety of behaviors including feeding, dwelling, protection, hunting and nesting (Fenton and Fenton, 1937; Osgood, 1970; Seilacher, 1970; Jensen, 1997; Mángano and Buatois, 2003a, 2004; Brandt, 2008).

Rusophycus from marine Paleozoic deposits mostly records the activity of trilobites or trilobitomorphs (e.g., Osgood, 1970; Crimes, 1975). Occurrences of *Rusophycus* in post-Paleozoic rocks and in freshwater deposits (e.g., Bromley and Asgaard, 1972; Minter et al., 2007) suggest that a wide variety of arthropods (e.g., notostracans, anostracans) can also produce these structures.

RUSOPHYCUS AEGYPTICUS (Seilacher, 1990)
Figure 10.1–10.3

Specimens.—Twenty five specimens on a bedding plane in Wadi Umm Jafna. Additionally, five specimens were found in Wadi Qunai.

Diagnosis.—Emended: relatively flat, small elongate *Rusophycus* with endopodal scratches prominent at the front and close to the axial area, and well developed external, mostly smooth, exopodal lobes. Faint extrovert exopodal brushings may be present in the rear part of lobes. In deeper specimens, the exopodal lobes are commonly separated from the endopodal ones by an oblique ridge (modified from Seilacher, 1990).

Description.—Elongate, relatively flat, heart-shaped bilobate hypichnial structures. Length is 22 to 35 mm. Width is 22 to 24 mm. Two main lobes are clearly defined: an internal lobe, very prominent in the anterior part and typically tapering towards the posterior part, and an external lobe, subparallel to the internal one and sometimes increasing in width towards the posterior part of the structure (Fig. 10.3). Lobes typically diverge anteriorly forming an anterior gap between prominent internal lobes. Transverse to slightly retroverse endopodal scratch marks occur in the internal lobe, flanked by mostly smooth external lobes (Fig. 10.3). Scratch marks are typically too small and indistinct to reveal morphologic details. An oblique ridge separates the internal and external lobes. A thin marginal ridge can be locally observed in a few specimens. On a large block from Wadi Umm Jafna, specimens of *Rusophycus* are clearly oriented and aligned (Fig. 10.1). Partially imbricated impressions best recording the anterior part of individual specimen form continuous rows (Fig. 10.1). *Rusophycus aegypticus* commonly intergrade with *Cruziana jordanica*.

Remarks.—Seilacher's (1990) original diagnosis of *Cruziana aegyptica* was based on *Rusophycus*-type trace fossils. However, *Rusophycus* is a distinct ichnotaxon and, thus, heart-shaped specimens are herein referred to *Rusophycus aegypticus*. Based on the presence of well-developed external exopodal lobes, *R. aegypticus* has been included in the *Cruziana semiplicata* group (Seilacher, 1992). *Rusophycus aegypticus* is morphologically close to *R. arizonensis* from the middle Cambrian Flathead Sandstone and the Tapeats Sandstone in United States (Seilacher, 1990, 1992). However, *R. arizonenesis* is typically more elongated than *R. aegypticus*, and commonly displays subparallel exopodal marks visible on exopodal lobes, and a more continuous marginal ridge (see Buatois and Mángano, 2011, fig. 13.5e). Moreover, the peculiar mode of occurrence of nested anterior impressions, forming continuous rows (Fig. 10.1), is unkown in *R. arizonensis*. Based on isolated specimens, however, distinction between *R. arizonensis* and *R. aegypticus* may be problematic.

RUSOPHYCUS CARBONARIUS (Dawson, 1864)
Figure 11.1, 11.2, 11.4

Specimens.—Several tens to hundreds of specimens on a block from Wadi Al Hisa and on slabs from Wadi Qunai from both the Hanneh Member and the lower part of the Umm Ishrin Formation.

Description.—Short bilobate, coffee bean-shaped structures commonly with parallel or rarely slightly oblique lobes. Preserved as positive hyporeliefs (Fig. 10.2, 10.4). Width is 4 to 12 mm but characteristically around 8 mm. Lobes are mostly smooth or rarely exhibit faint transverse indistinct striations.

Remarks.—*Rusophycus carbonarius* is regarded as the most stable ichnospecies of small, simple, typically coffee-bean shaped *Rusophycus* (Keighley and Pickerill, 1996; Schlirf et al., 2001). *Rusophycus carbonarius* is considered as a resting trace of small arthropods. In the analyzed material, *Rusophycus carbonarius* intergrades with *Cruziana problematica*. Accordingly, it can be inferred that they were produced by the same organism.

RUSOPHYCUS BURJENSIS n. isp.
Figure 12.1, 12.3, 12.5

Specimens.—Four slabs (FG 603 F_01, FG 603 Z_02, FG 603 Z_01, FG 603 Q_03) from Wadi Fifa, Zerqa Ma'in, and Wadi Qunai containing four specimens and approximately 35 specimens observed in at Wadi Qunai, Wadi Issal and Zerqa Ma'in.

Type.—Holotype, FG 603 Z_01, Zerqa Ma'in (Fig. 12.1).

Etymology.—Referring to its distinctive presence in the Burj Formation.

Diagnosis.—Large convex *Rusophycus*, displaying distinct endopodal scratches that are dominantly transversal. Anterior part commonly slightly wider than posterior part. Lobes may gap slightly anteriorily. Rarely, specimens display a subtle differentiation between anterior, proverse scratches, and posterior, transverse scratch marks. Claw formula exhibits one major claw and up to four secondary claws.

Description.—Slightly to distinctively elongated, medium- to large-sized, strongly convex bilobate structures with well-developed endopodal scratch marks; preserved as positive hyporelief. Anterior part wider than the posterior part (Fig. 12.1, 12.5). Lobes dominantly subparallel, slightly diverging at the anterior part (Fig. 12.5). Scratch marks transverse, rarely showing gradual transition to slightly proverse scratch marks towards the anterior part (Fig. 12.3). A characteristic gap is observed between clusters of proverse and transverse scratch marks. Typically one main claw with two to three, rarely four secondary, claw marks (Fig. 12.3). There is a gradual decrease in

the size of the scratch marks towards the posterior part. Length is 55 to 160 mm and width is 45 to 130 mm. Maximal burrow depth is about 35 mm.

Remarks.—Although Seilacher (1990) erected *Cruziana salomonis* based on mostly cruzianiform specimens he also included *Rusophycus*-type burrows in this ichnospecies. Since *Rusophycus* is regarded as separate from *Cruziana*, *Rusophycus burjensis* is herein proposed for the rusophycid expression of *Cruziana salomonis*. *Rusophycus burjensis* is characterized by pronounced, transversal to slightly proverse front leg digging marks (Fig. 12.3). In more convex specimens (e.g., Fig. 12.1), a more pronounced differentiation between more proverse front leg diggings marks and mainly transversal to slightly retroverse digging marks can be observed. In our material, endopodal scratches are dominant and exopodal brushings are virtually absent which suggests a strict prosocline burrowing attitude (cf. Seilacher, 1990).

Rusophycus cf. R. leifeirikssoni (Bergström, 1976)
Figure 13.1, 13.2

Specimens.—One specimen on slab (FG 603 T_06) recovered as float from hill slope in Wadi Uhaymir.

Description.—Deep bilobate structure with a round to apple-shaped outline preserved as positive hyporelief. Length is 34 mm. Width is 31 mm. Depth is 33 mm. Lobes are almost vertical, perpendicular to the bedding plane. Presumed anterior part deeper and narrower than posterior part (Fig. 13.1). Lobes mostly smooth, with poorly preserved scratch marks perpendicular to the axis (Fig. 13.2). Individual claw impressions are not discernible. Markings of cephalon and genal spines are lacking.

Remarks.—The ichnotaxonomy of deeply excavated *Rusophycus* with sub-equal width and length is problematic. Essentially, two ichnospecies are formally recognized: *Rusophycus leifeirikssoni* from the lower Cambrian to Tremadocian of Gondwana, and *R. jenningsi* from the lower Cambrian of Laurentia. *Rusophycus jenningsi* is a prosocline structure characterized by a wider anterior end displaying common headshield markings resulting from the shovelling down motion into the sediment (Jensen, 1997; Seilacher, 2007). *Rusophycus leifeirikssoni* from Newfoundland was interpreted by Bergström (1976) and subsequently Seilacher (1985, 1992, 2007) as an opisthocline (tail down) structure. However, analysis of the ornamentation of these deep *Rusophycus* by Fillion and Pickerill (1990) clearly shows that the deepest part displays cephalic impressions and the structure is prosocline. This burrowing attitude has been confirmed by detailed morphologic analysis of specimens of *R. leifeirikssoni* from northwest Argentina (Mángano and Buatois, 2003a, 2004; Seilacher, 2007, pl. 11). Another comparable form is *Cheiichnus* which lacks a clear bilateral symmetry and is interpreted as the result of rotational movement of trilobites in deep prosocline burrows (Jensen and Bergström, 2000).

Recognition of burrowing attitude in deep *Rusophycus* is difficult if markings of the exoskeleton are absent and scratch-mark ornamentation is poorly preserved. The deep structure described herein displays a bilobated form (i.e., does not fit into *Cheiichnus*) but no cephalic markings are observed, and the scratch mark ornamentation is sparse and indistinct. However, the Hanneh specimen seems to be narrowest at its deepest part and, thus, it is consistent with some of the diagnostic features of *R. leifeirikssoni* (cf. Bergström, 1976; Seilacher, 1992; Mángano and Buatois, 2003a). Mángano and Buatois (2003a, 2004) documented *R. leifeirikssoni* in intertidal deposits of Gondwana and proposed either feeding or nesting behavior. Other authors suggested that *R. leifeirikssoni* may reflect predation on worms since specimens of this ichnospecies are locally associated with *Planolites*, *Palaeophycus*, or *Gyrolithes* (Fillion and Pickerill, 1990). However, there is no detailed study of *R. leifeirikssoni* similar to those performed in *R. dispar* (see Jensen, 1997), and many vermiform structures seem to cross-cut *Rusophycus* suggesting revisiting by deposit feeding worms exploiting an enriched sediment infill.

Rusophycus isp.
Figure 11.3–11.6

Specimens.—Six specimens in a large block at the uppermost part of the Hanneh Member in Wadi Al Hisa. It has also been observed in the lower levels of the overlying Umm Ishrin Formation at the same locality.

Description.—Very elongate, relatively large *Rusophycus* preserved as hypichnial ridges. Length is 56 to 110 mm. Maximum width is 28 to 45 mm. Individual lobes are subparallel and tapered posteriorly. Lobes are well-defined and separated by a deep central groove (Fig. 11.4, 11.6). Lobes covered by delicate, imbricated sediments pads displaying eight to 10 thin, subparallel scratch marks forming an acute angle ($<60°$) to almost subparallel to the axial groove (Fig. 11.5). Sediment pads define wrinkles transversal to the axial groove. In a few specimens, the rusophycid morphology is not well developed. Lobes intersect each other, forming shorter, linear structures without clear axial termination (Fig. 11.3). These specimens tend to display imbricated sediment pads almost perpendicular to the sediment surface, producing distinctive transverse ridges. Specimens are commonly more penetrative than the associated *C. problematica* and *R. carbonarius* but are sometimes cross-cut by the latter.

Remarks.—This form displays significant similarities in claw formula with *C. nabataeica* (Seilacher, 1990). The claw formula is characterized by multiple, typically eight to 10, subparallel delicate ridges that are best interpreted as exopodal brushings. It also shows imbrication of sediment pads displaying distinctive sets brushings as observed in *C. nabataeica*. However, the *Rusophycus* specimens herein described are considerably larger, more elongated, and display a well-defined, deeper axial depression than the material illustrated as *C. nabataeica* from Petra, Jordan (cf. Seilacher, 1990, pl. 32.5, pl. 32.1a). Rusophycid specimens of *Cruziana fasciculata* are similar in shape and size range to the analyzed material. However, *C. fasciculata* displays a clear trend, from transverse scratch marks in the anterior part to strongly retroverse in the posterior part. This trend is absent in the Hanneh Member material. Specimens displaying a linear morphology are strikingly similar to the material illustrated by Seilacher from Sinai (1990, pl. 32.1b).

Arthropod Trackways and Scratch Marks
Ichnogenus Dimorphichnus Seilacher, 1955

Remarks.—*Dimorphichnus* comprises asymmetrical trackways involving two types of imprints: elongated scratches or raker marks and blunt imprints referred to as pusher marks (Seilacher, 1955). In case of partial preservation (i.e., undertrack fallout), the distinction from the related ichnogenus *Monomorphichnus* is difficult. Both ichnotaxa are in need of revision (see discussion on *Monomorphichnus*). *Dimorphichnus* characteristically exhibits numerous repetitive and overlapping sets of scratch-like, sinusoidal, curvilinear or straight rakers opposing sets of blunt pushers, which are typically lacking in *Monomorphichnus*.

Dimorphichnus is attributed to the grazing activity of trilobites. The pusher marks are suggested to reflect a stabilizing motion of walking legs of the trilobite whereas the opposite legs stirred up sediment and detritic food particles (Seilacher, 1955) producing the rakers.

Dimorphichnus cf. D. obliquus
Figure 14.3

Specimens.—Fifteen specimens observed on slab FG 603 I_06,

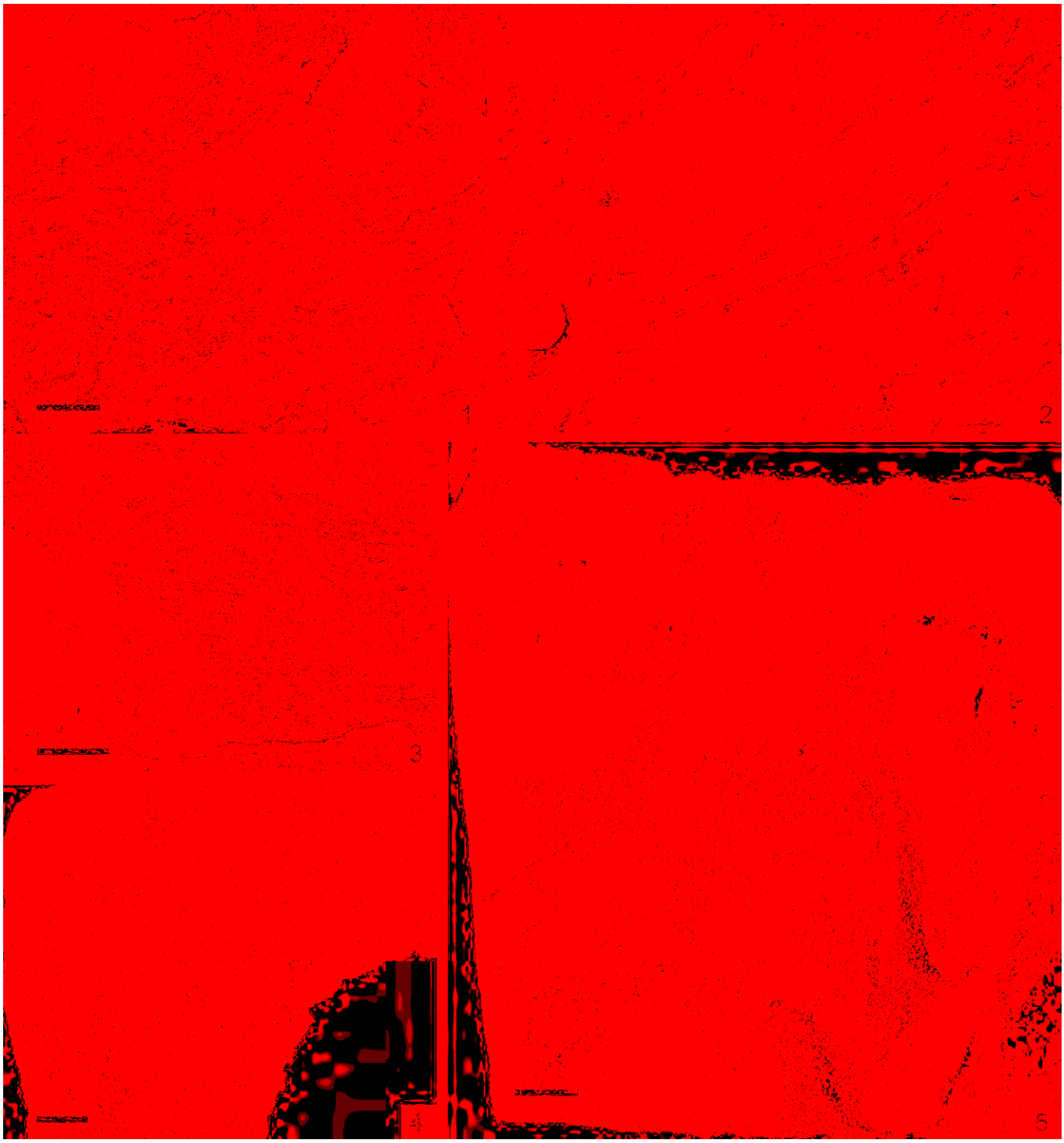

FIGURE *14*—Trackways and Scratch marks, Hanneh Member. *1*, *Monomorphichnus* isp. B, scale=5 cm, Wadi Uhaymir, coin diameter is 28 mm; *2*, *Monomorphichnus* isp. C, positive hyporelief on the block from Wadi Al Hisa, coin diameter is 28 mm; *3*, *Dimorphichnus* cf. *obliquus*. FG 603 T_11, float from Wadi Uhaymir, scale=2 cm; *4*, indeterminate scratch marks, FG 603 T_03, float from Wadi Uhaymir, scale=1 cm; *5*, *Monomorphichnus* isp. A., Wadi Uhaymir, FG 603 T_09, scale=1 cm.

FG 603 T_11, FG 603 T_05, and FG 603 T_12 from Wadi Issal and Wadi Uhaymir.

Description.—Straight to sigmoidal scratch marks preserved as positive hyporelief. Morphology reveals mostly two main ridges rarely accompanied by two secondary scratches. Two main scratches are typically equidistant or locally seem to converge in one direction. The relief of the ridges commonly decreases within one set. Scratch length is 30 to 70 mm but most commonly is around 50 mm. Distance between main scratch marks is up to 1 mm.

Remarks.—The presence of two main scratch marks makes this form at first sight comparable to *Dimorphichnus bilinearis*. However, as *Dimorphichnus* is always preserved as hypichnial

undertracks, the undertrack fallout effect commonly results in a decrease of the number of scratch marks, and large slabs are required to confidently determine the claw formula. Under close inspection, the analyzed material locally comprises more than two main ridges within one set, displaying a couple of secondary scratch marks. This particular claw formula of two principal scratch marks associated to two minute secondary ones is diagnostic of *D. obliquus* (Seilacher 1955, 1990). This form is quite common in the Hanneh Member, and is typically associated with *Cruziana salomonis* and *Rusophycus burjensis*, suggesting a common producer. Seilacher (1990) related *C. salomonis* and its rusophycid variants to *D. quadrifidus*, characterized by four subequal scratch marks in rakers. As outlined by Jensen (1997), not only the number but also the morphology and size of the scratch marks can be affected in undertracks. In short, considering preservational constrains, the analyzed material is closest to *D. quadrifidus*. Although scratch marks are clearly sigmoidal, no clear pusher marks have been identified in any of the analyzed slabs.

Ichnogenus Diplichnites Dawson, 1873

Diplichnites isp.

Specimens.—Six specimens on a bedding plane in the lower interval of the Wadi Uhaymir section.

Description.—Subaparallel rows of tracks consisting of series of up to seven predominantly elongate to more rarely ellipsoidal oblique imprints preserved as negative epirelief. Imprints vary between 1 to 5 mm long but are relatively uniform in size within the row. Imprint pace is 7 to 11 mm and relatively uniform within one series. Internal width is 31 mm. External width is 58 mm. These two characteristics are observed in only one specimen that includes three series in one row with only one series forming an opposite row. Imprints of opposing series are markedly smaller suggesting a slightly asymmetrical trackway. Set overlap, including two to three imprints, is 21 mm. Repeat distance is 47 mm. Set length is 68 mm. Reconstructed trackway length is up to 140 mm. Angle between series line and imprint is approximately 25°.

Remarks.—The basic morphologic arrangement of the specimens described herein best fit within *Diplichnites* simple trackways consisting of two parallel rows of tracks oriented approximately perpendicular to the midline (Buatois et al., 1998). Because of the unclear status of the different *Diplichnites* ichnospecies and fragmentary nature of the studied material, the Jordan specimens are classified only at ichnogeneric level. Lower Paleozoic examples, probably produced by trilobites, were included in *Diplichnites* by Seilacher (1955).

Ichnogenus Monomorphichnus Crimes, 1970

Remarks.—In the original description of *Monomorphichnus*, Crimes (1970) referred to trace fossils observed by Martinsson (1965) who suggested trilobites "caught up in the current" producing these scratch marks by raking up the sediment surface with their endopodites. This interpretation was subsequently endorsed by Osgood (1970). Hence, Crimes (1970) removed scratch marks that lack the diagnostic pusher imprints from the ichnogenus *Dimorphichnus*, suggesting that *Monomorphichnus* illustrates a different behavior. Seilacher (1985, 1990) considered *Monomorphichnus* to be a junior synonym of *Dimorphichnus,* since *Monomorphichnus* was considered to document an alternative preservation of *Dimorphichnus* (Goldring and Seilacher, 1971). Seilacher (1985) indicated that the type material of *Monomorphichnus* displays pusher marks. However, this view was rejected by Fillion and Pickerill (1990). Jensen (1997) noted that the laterally repeated ridges seen in the holotype illustrated by Crimes (1970) are partly overlapping. Assuming a genetically related origin, Jensen (1997) considered specimens described by Crimes (1970) as of *Dimorphichnus*-type. Mángano and Buatois (2003b) noted that if *Monomorphichnus*-type material is *Dimorphichnus*-like, then many structures presently included in *Monomorphichnus* will not be easy to relocate in *Dimorphichnus* or in other available ichnogenera, which would require erection of a new substitute ichnotaxon. Accordingly, *Monomorphichnus* is provisionally retained, following Jensen (1997), to embrace sets of "monomorphic" scratch marks that exhibit distinctive morphology, and cannot be placed in other arthropod-produced ichnogenera (Mángano et al., 2005).

In lower Paleozoic shallow-marine deposits, *Monomorphichnus* is mostly attributed to trilobites (e.g., Crimes and Anderson, 1985; Fillion and Pickerill, 1990; Jensen, 1997).

Monomorphichnus isp. A

Figure 14.5

Specimens.—Four specimens observed on slab FG 603 T_09 in Wadi Uhaymir.

Description.—Sets of up to five elongate, slightly curved or sigmoidal, subequal ridges arranged in bundles and preserved as positive hyporeliefs. Most bundles, however, display groupings of four subequal scratch marks. A few prominent scratch marks are accompanied by one to two secondary scratch marks. Locally, some ridges may show a tiny distal bifurcation. Length of individual ridges is 8 to 25 mm, commonly 15 to 20 mm. Width of principal ridges is 1 mm whereas that of secondary ridges is around 0.5 mm.

Remarks.—Scratch marks in the best preserved bundle in slab T-09 (Fig. 14.5, central one) seem to converge towards one end. However, this may be an artifact related to the irregularity of the surface rather than true convergence as the other scratch marks are essentially subparallel. *Monomorphichnus* is considered to reflect incidental scratching by arthropods affected by currents rather than systematic browsing behavior, as is proposed for *Dimorphichnus* (Osgood, 1970). Neither the morphology of the scratch marks nor the distribution of the bundles is reminiscent of *Dimorphichnus*. The slab analyzed comprises some flute marks indicating erosive currents. It is uncertain, however, if the animal was under the effect of the current that produced the flute-like structures.

The fact that many of the bundles in the analyzed slab record groupings of four scratch marks, locally accompanied by secondary claw marks, suggests that the producer of these scratch marks may have also been the producer of *C. salomonis and R. burjensis*.

Monomorphichnus isp. B

Figure 14.1

Specimens.—One specimen observed in the field in Wadi Uhaymir.

Description.—Set of eight parallel, straight to slightly curved subequal ridges preserved as positive hyporelief. Ridges are equidistant and 35 to 40 mm long. Spacing between ridges is about 2 mm. Ridges are up to 2 mm wide but commonly around 1 mm.

Remarks.—No clear pusher marks have been observed. Although, scratch mark sets display a sigmoidal to curved morphology (particularly the larger ones) reminiscent of rakers. The distribution of sets of scratch marks is disorganized and devoid of a clear *Dimorphichnus*-like pattern (i.e., laterally repeated sets of rakers or rakers and pushers forming laterally alternating rows). The claw formula clearly differs from that of *C. salomonis*, *R.burjensis*, and probably *Monomorphichnus* isp. A, suggesting a different arthropod producer.

Monomorphichnus isp. C

Figure 14.2

Specimens.—One specimen on a block from Wadi Al Hisa.

Description.—Set of five, large, long individual parallel ridges preserved as positive hyporelief. Width is 1 to 4 mm and variable

along individual ridges but typically around 2 mm. Length of ridges is 150 to 220 mm. Spacing between individual ridges is 6 to 11 mm but is commonly around 8 mm.

Remarks.—This form is characterized by relatively long, prominent simple scratch marks recording the activities of a large arthropod. Interestingly, the best-preserved specimen is an isolated set associated to tiny cruzianids (*C. problematica* and *R. carbonarius*) that completely cover the surface of the slab. This suggests that *Monomorphichnus* isp. C may record feeding of large benthic or nektonic arthropods browsing on the sediment surface in search of small prey. Unfortunately, other occurrences of *Monomorphichnus* isp. C are associated with dense, poorly preserved palimpsestic surfaces, and a genetic association with small cruzianids cannot be confirmed.

Indeterminate Scratch Marks
Figure 14.4

Specimens.—Two specimens on slab FG 603 T_03 collected from float in Wadi Uhaymir.

Description.—Series of up to seven relatively even-spaced deep imprints preserved as positive hyporelief. Imprint morphology either blunt, cone-shaped to comb-shaped comprising up to four subparallel claw marks (Fig. 14.4). Widest diameter of individual imprints is 6 to 10 mm but is typically 9 mm. The distance between consecutive imprints is 3 to 6 mm. On slab FG 603 T_03, two partially overlapping series of imprints are recognized.

Remarks.—In the material studied, two partially superimposed series of imprints are observed. The series seem to form a row of impressions of one side of the body of the producer, recording partial preservation of a *Diplichnites*-like structure. Alternatively, these imprints may present pronounced pusher marks of *Dimorphichnus* cf. D. *quadrifidus*, in which the raker marks are absent due to incompleteness of the slab or undertrack fallout. Interestingly, the material analyzed herein shows some general similarity with specimens from the Silurian of Libya described by Seilacher (2005) as 'diplichnitiform' version of *Cruziana bonariensis* (p. 131, fig. 1d, p. 136, fig. 4). However, the interpretation as *Diplichnites*-type trackway is difficult as the individual imprints are considerably deep and the non-preservation of the opposite row appears enigmatic. In short, a confident ichnogeneric assignment is not possible. The most likely producers are trilobites with four-clawed endopodites, as suggested by quadrifid claw formula adding to the structures potentially produced by the tracemakers of *Cruziana salomonis* and *Rusophycus burjensis* in the Hanneh Member.

PALEOECOLOGIC AND PALEOENVIRONMENTAL SIGNIFICANCE OF TRACE-FOSSIL ASSEMBLAGES

Eleven trace-fossil assemblages have been identified: *Arenicolites* isp., *Diplocraterion* isp., fugichnia, *Rosselia* isp., *Gyrolithes polonicus*, *Gordia marina*, *Bergaueria sucta*, *Cruziana salomonis*, *Rusophycus aegypticus*, *Cruziana problematica*, and *Archaeonassa fossulata* assemblages (Fig. 15). Arthropod trackways and scratch marks are clearly abundant in the uppermost part of the Hanneh Member and well into the overlying Um Ishrim Formation. Ichnotaxa represented by specimens found as float material are not included in any assemblage. Trace-fossil assemblages are characterized in terms of ichnotaxonomic composition, style of preservation, ethology, trophic types, and tiering structure. Trace-fossil assemblages do not necessarily represent communities. Some assemblages may record the superimposition or more than one community whereas others may represent variations related to lateral heterogeneity within an individual community (e.g., *Gordia marina* and *Archaeonassa fossulata*). Degree of bioturbation in cross-section is assessed following the scheme by Taylor and Goldring (1993) which comprises seven categories of bioturbation index (BI 0–6). Where possible, the percentage of bioturbation on bedding planes has been estimated in the field, using the bedding-plane bioturbation indices (BP-BI 1–5) proposed by Miller and Smail (1997). Assemblages are analyzed in the conof their associated facies in order to integrate ichnologic and sedimentologic information for evaluation of ecologic controls and depositional environments (Fig. 15). Each of these trace-fossil assemblages reveals a close link between benthic faunas and the prevailing environmental conditions in the analyzed delta-shelf system.

Arenicolites *isp. assemblage*.—The *Arenicolites* assemblage consists of *Arenicolites* isp., *Palaeophycus tubularis*, and *Skolithos linearis*. This assemblage occurs in trough cross-bedded and tabular cross-bedded fine- to medium-grained sandstone forming moderate-size tidal bars, compound dunes and simple dunes, intercalated with heterolithic intervals (Fig. 4.1). Reactivation surfaces, arrangement in bundles, herringbone cross-stratification, rip-up clasts, and single and double mudstone drapes collectively argue for tidal dominance. Interestingly, large-scale tidal sandbodies, such as those present in the Zerqa Ma'in section, are typically devoid of the *Arenicolites* assemblage. Circular openings that represent either *Skolithos linearis* (Fig. 4.6) or partially preserved *Arenicolites* isp. occur on bedding planes with oscillatory ripples. The *Arenicolites* assemblage occurs in the lower interval of the Hanneh Member in the Wadi Issal and Wadi Uhaymir sections.

The assemblage is dominated by domichnia of suspension feeders although predation may have been involved as well. Some occurrences of this assemblage consist of monospecific suites of *Arenicolites* isp. of similar size. In these cases, deposits are sparsely bioturbated (BI 1). In the case of slightly more diverse suites containing also *Skolithos linearis* and *Palaeophycus tubularis*, there is a remarkable increase in the degree of bioturbation (BI 4–5). The assemblage has a simple tiering structure consisting of shallow-tier *Palaeophycus tubularis* and deep-tier *Arenicolites* isp. and *Skolithos linearis*.

The dominance of dwelling burrows of suspension feeders and the association with sedimentary structures recording dune migration clearly indicate moderate to relatively high-energy subtidal environment affected by tidal currents with more diverse and densely bioturbated units recording the lower end-member of the energy spectrum. The fact that suspension feeding seems to have been the dominant trophic type suggests that turbidity in the water column was not a constraint. In contrast, in environments affected by deltaic progradation, suspension feeding tends to be suppressed because suspended river-born mud clogs the filter-feeding apparatuses of the benthic fauna (Gingras et al., 1998; MacEachern et al., 2005; Buatois et al., 2003, 2008). In fact, this tidal dune and sandbar complex seems to have been unrelated with the overlying delta because it occurs at the base of the Hanneh Member, overlying the transgressive limestone and stratigraphically below the prograding deltaic interval. Similar ichnofaunas in Cambrian tidal sandbodies were recently documented in the Gog Group of the Canadian Rockies by Desjardins et al. (2010) who proposed a number of taphonomic pathways for ichnofabrics dominated by vertical burrows in tide-dominated shallow-marine environments. In the Hanneh sea, during times of continuous bar and dune migration under the action of vigorous currents, organisms were unable to colonize the shifting substrate. In contrast, more protected settings allowed the establishement of an opportunistic suspension-feeding infauna during short-term periods of relative quiescence (Pollard et al., 1993). The similar size of the *Arenicolites* isp. specimens in the monospecific occurrences is also suggestive of a single colonization event. The

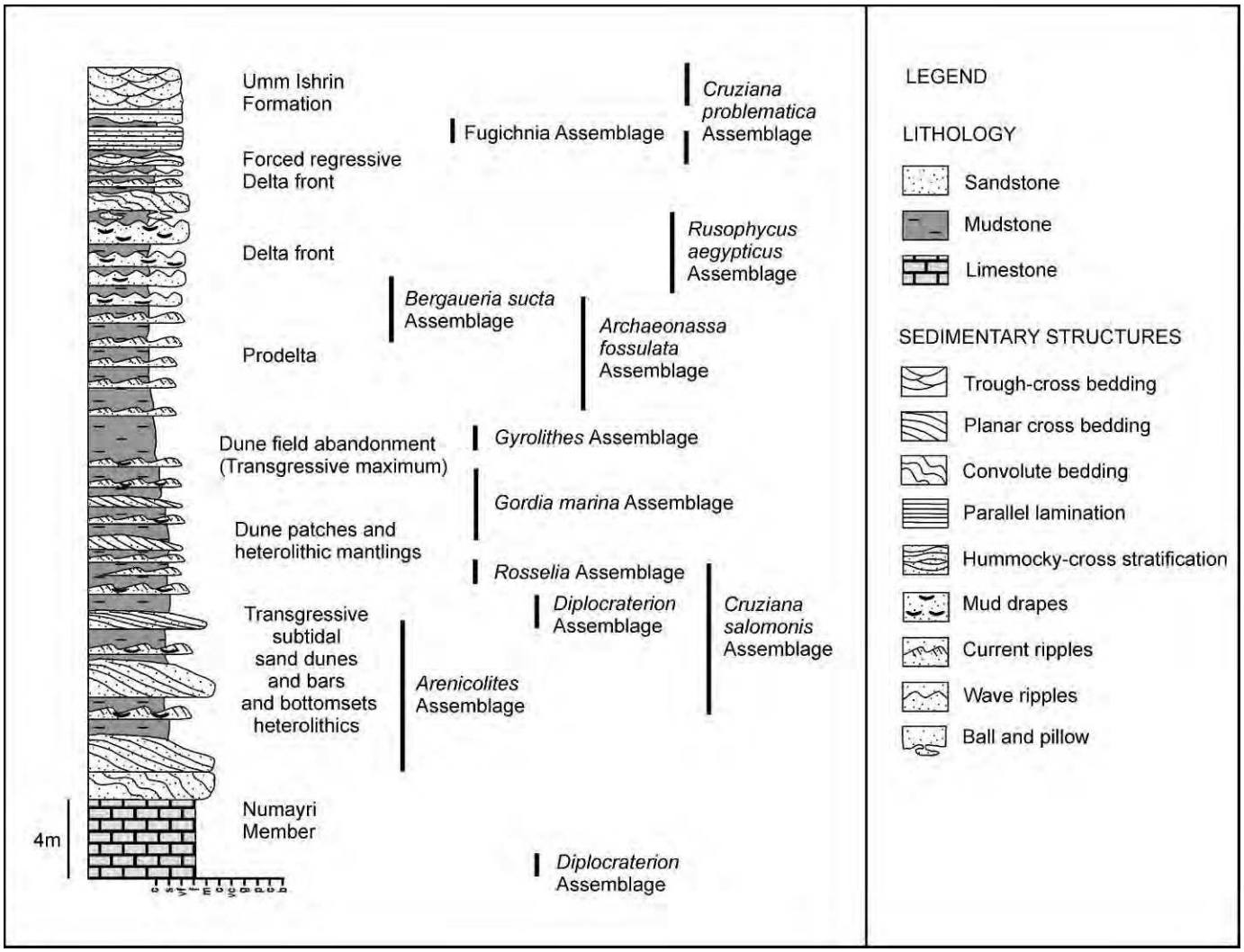

FIGURE 15—Composite section of the Hanneh Member showing the distribution of sedimentary facies and trace-fossil assemblages.

increase in ichnodiversity and the sharp increase in degree of bioturbation in some occurrences of this association reveal slightly more continuous colonization windows and probably dune and bar abandonment under lower-energy conditions.

Diplocraterion *isp. assemblage*.—The *Diplocraterion* assemblage consists of monospecific suites of *Diplocraterion* isp. It is sparsely recorded in planar and trough cross-bedded, and current ripple-laminated fine- to medium-grained sandstone. This assemblage occurs in the lower interval of the Hanneh Member at the Wadi Uhaymir section (Fig. 4.4). In Wadi Umm Jafna, a similar assemblage occurs near the contact between the Tayan Member and the Numayri Member. These deposits most likely record sedimentation in small compound dunes. As in the case of the facies containing the *Arenicolites* assemblage, herringbone cross-stratification and mudstone drapes indicate tidal processes.

The assemblage is dominated by equilibrichnia of suspension feeders. This monospecific assemblage has a strong taphonomic overprint as only the deepest parts of *Diplocraterion* are preserved. Tiering position is difficult to reconstruct. The actual depth of bioturbation is not possible to evaluate due to the dumb-bell preservation of *Diplocraterion* isp. (burrows protruding up to 13 mm from the sandstone sole); some shallower structures may have been wiped out by erosion. In any case, judging from comparisons with similar ichnofabrics elsewhere (e.g., Mángano and Buatois, 2004), relatively deep-tier emplacement is most likely. Density of *Diplocraterion* isp. on bedding planes is moderate (BP-BI 3).

The integration of ichnologic and sedimentologic evidence suggests that in the Burj Formation the *Diplocraterion* assemblage may be related to two different contexts. In the lower Hanneh Member, the *Diplocraterion* assemblage occurs in a transgressive tidal-dune complex which is stratigraphically below the prograding deltaic interval. In this case, colonization took place in a relatively high-energy setting affected by tidal erosion (i.e., autogenic origin). However, the *Diplocraterion* assemblage also occurs in transgressive erosional surfaces characterizing the initial phases of transgression of the Numayri Member (i.e., allogenic origin). In Wadi Umm Jafna, the *Diplocraterion* assemblage is associated with several coarse-grained sandstone transgressive lags at the transition between the Tayan and Numayri members. The apparent monospecific nature of the assemblage and the moderate densities suggest opportunistic colonization due to short-term colonization windows.

Fugichnia assemblage.—The fugichnia assemblage comprises isolated occurrences of escape trace fossils in parallel-laminated fine- to medium-grained sandstone. These deposits reflect rapid sedimentation due to sheet floods under upper-flow regime in a

delta front. This assemblage occurs near the top of the Wadi Uhaymir section within a stratigraphic interval displaying strong synsedimentary deformation, further supporting rapid sedimentation. Most of the parallel-laminated fine-to medium-grained sandstone deposits are unburrowed and only locally sparse bioturbation (BI 1) is present. Interbedded mudstone is moderately bioturbated, suggesting abundant benthic life previous to the deposition of the sandstone. The occurrence of escape trace fossils is consistent with episodic deposition and a drastic increase of fluvially derived clastics into the system. These escape structures are the result of collapse and sediment failure as the animal moved upwards in a rapidly aggrading bed (Buck and Goldring, 2003).

Rosselia *isp. assemblage*.—The *Rosselia* assemblage is dominated by *Rosselia* isp. *Asterosoma* isp., *Planolites montanus,* and *Palaeophycus tubularis* are subordinate components. This assemblage occurs in siltstone and current-ripple cross-laminated very fine- to fine-grained sandstone forming heterolithic intervals characterized by flaser, wavy, and lenticular bedding. Mudstone drapes and syneresis cracks are commonly present. In the Hanneh Member, these heterolithic deposits occur above the small tidal dunes hosting the *Diplocraterion* assemblage and below an interval characterized by dune-patch deposits. They most likely record fluctuating energy and alternating traction and suspension fallout under tidal influence in areas located between the tidal dunes. The *Rosselia* assemblage is present near the top of the lower interval of the Hanneh Member in the Wadi Uhaymir, Wadi Issal, and Wadi Qunai sections.

Rosselia isp. records dwelling/equilibrium burrows of detritus-feeding organisms. Feeding traces of deposit feeders are represented by *Planolites montanus* and *Asterosoma* isp. Although a direct transition between *Rosselia* and *Asterosoma* has not been observed, in the Wadi Issal section *Asterosoma* locally displays highly inclined components that suggest gradation with *Rosselia*. Suspension feeding and/or active predation is only indicated by the presence of *Palaeophycus tubularis* which may locally form dense occurrences. Deposits containing the *Rosselia* assemblage are sparsely to moderately bioturbated (BI 1–4, but typically 3). This assemblage has a relatively simple tiering structure consisting of a shallow tier with *Planolites montanus*, *Asterosoma* isp. and *Palaeophycus tubularis*, and a deep-tier represented by *Rosselia* isp. In cross-sectional views, *Rosselia* pillar-like structures are observed to cross-cut shallower elements that create a mottled background fabric (Fig.5.3, 5.4). In the Hanneh Member, the presence of deep, only slightly bulging structures, recording continuous relocation of the trace maker, is consistent with periodic, high rates of sedimentation.

The dominance of vertical burrows of detritus feeders and horizontal feeding burrows of deposit feeders suggests low- to moderate-energy conditions. In particular, the very long, pillar-like specimens of *Rosselia* isp. are comparable to stacked *Rosselia* of Nara (2002), and suggest vertical burrow adjustments in response to sedimentation events. However, the more or less cylindrical structures of *Rosselia* isp. differ from the classic examples of *Rosselia socialis*. Several studies have documented variable morphologies of *Rosselia* in response to sedimentation events (e.g., Nara, 1997, 2002; Pemberton et al., 2001; Campbell et al., 2006). In a pioneer study, Nara (1995, 1997) described funnel- and spindle-shaped specimens of *Rosselia* which are vertically stacked reflecting upward migration to avoid burial due to episodic sedimentation in a storm-dominated shallow-marine setting. Pemberton et al. (2001) illustrated stacked funnel-shaped *Rosselia* as a response of storms in a lower shoreface. Campbell et al. (2006) documented *Rosselia* of simple morphology in river-derived oceanic-flood mudstone and siltstone which they interpreted as recording adaptation to thrive under conditions of very high sedimentation rate that caused the exclusion of any other benthic fauna. *Rosselia* has been recently documented in tidal sandbodies emplaced in the distal delta-front of a tide-dominated delta (Carmona et al., 2009).

Gyrolithes polonicus *assemblage*.—The *Gyrolithes polonicus* assemblage consists of a monospecific occurrence of this ichnotaxon. This assemblage occurs at the base of a massive fine-grained sandstone bed, penetrating into the underlying mudstone. The underlying mudstone records the final abandonment of the tidal-dune field. The *Gyrolithes polonicus* assemblage is present below the maximum flooding surface in the upper part of the middle interval of the Hanneh Member in the Wadi Uhaymir section.

This assemblage is characterized by dwelling structures that may have served for variable purposes (Netto et al., 2007). Specimens are unlined, subcircular in cross-section, and passively filled with sediment introduced from the overlying sandstone. The spiral structures are not deeply penetrative. The associated degree of bioturbation is moderate (BI 3).

All these features indicate that the Hanneh *Gyrolithes* were constructed as open burrows in cohesive muddy substrate. As such, the *Gyrolithes polonicus* assemblage might be regarded as an example of the *Glossifungites* ichnofacies. A link between *Gyrolithes* and cohesive substrates has been documented in recent studies (Netto et al., 2007; Wetzel et al., 2010). Interestingly, there is no evidence that allows us to link this occurrence to erosional exhumation as it is typical for the *Glossifungites* ichnofacies of siliciclastic settings (MacEachern et al., 1992, 2007). The shallow penetration of the spirals into the mudstone could indicate erosion of the upper parts of the burrows. However, no burrow truncation is clearly observed, and *Gyrolithes polonicus*, in contrast to other younger ichnospecies, is typically shallow and consisting of few whorls (e.g., Jensen, 1997; Droser et al., 2002, 2004). Most likely, this occurrence of the *Glossifungites* ichnofacies may be linked to the widespread development of relatively firm substrates as a result of limited extent and depth of bioturbation in the absence of a well-developed mixed layer during the early Paleozoic (Droser et al., 2002, 2004; Dornbos et al., 2004, 2005; Jensen et al., 2005).

Gordia marina *assemblage*.—The *Gordia marina* assemblage is dominated by *Gordia marina* and *Helminthoidichnites tenuis*. *Diplichnites* isp. is a subordinate form. This assemblage is present at the top and the base of thinly bedded very fine- to fine-grained sandstone, with current ripples, flaser bedding and mudstone drapes, interbedded with mudstone. These heterolithic deposits occur between and above layers forming discrete sand-dune patches. The *Gordia marina* assemblage occurs in various stratigraphic levels near the base of the middle interval of the Hanneh Member in the Wadi Uhaymir, Wadi Umm Jafna, and Wadi Issal sections.

This assemblage is characterized by simple grazing trails (*Gordia marina* and *Helminthoidichnites tenuis*) of vermiform organisms, as well as by a smaller proportion of arthropod trackways (*Diplichnites* isp.). Detritus feeding and very shallow deposit feeding are the inferred trophic types involved in this assemblage. The trails and tracks are superficial to shallow-tier bedding-plane parallel structures with essentially no distubance of the primary sedimentary fabric. Density on bedding planes is low (BP-BI 2), typically with patchy distribution.

The *Gordia marina* assemblage primarily records exploitation of nutrient-rich laminae that accumulated during slack-water times, most likely reflecting short-term colonization windows. This assemblage records colonization of the low-energy fine-grained deposits emplaced between areas of higher-energy

conditions characterized by the establishment of dune patches (see Desjardins et al., 2012).

Bergaueria sucta *assemblage*.—The *Bergaueria sucta* assemblage is dominated by *Bergaueria sucta*, *Palaeophycus tubularis, Planolites montanus, Rusophycus burjensis*. Poorly preserved arthropod scratch marks are present locally. This assemblage occurs in current-ripple cross-laminated very fine-grained sandstone at the upper interval of the Hanneh Member in the Wadi Uhaymir and Wadi Issal sections.

This assemblage reflects a combination of ethologies and trophic types, including dwelling, feeding and resting of suspension and deposit feeders. Two expressions of *Bergaueria sucta* are observed in the Jordan material. The first type consists of predominantly large specimens with well-developed lateral displacement that occur at the base of thin-bedded ripple cross-laminated sandstone, while the second type is represented by rather small single disc-shaped impressions preserved as casts at the base of erosionally based sandstone. Density on bedding planes is relatively high (Fig. 8.1; BP-BI 3 and locally 4) in the case of specimens with well-developed lateral displacement. Based on cross-cutting relationships, the tiering structure can be reconstructed as consisting of a shallow tier with *Bergaueria sucta*, *Palaeophycus tubularis* and *Planolites montanus*, cross-cutting each other, and a slightly deeper tier represented by *Rusophycus burjensis* (invariably cross-cutting shallower-tier structures).

The *Bergaueria sucta* assemblage characterizes an environment with fluctuating energy levels. The occurrence of *B. sucta* indicating lateral displacement most likely records relatively low-energy levels and low vertical accretion of the sea floor. This pattern resembles the horizontal repetition displayed by the ophiuroid resting trace *Asteriacites lumbricalis* (Seilacher 1953; Mángano et al., 1999). The occurrence of isolated sucker discs of *B. sucta* at the soles of erosionally based sandstone beds suggests that the organisms may have been swept off by currents. This assemblage occurs in prodelta to distal delta-front settings typically recorded in the upper Hanneh Member (Fig. 15).

Cruziana salomonis *assemblage*.—The *Cruziana salomonis* assemblage is an arthropod-dominated suite composed of *C. salomonis* and *Rusophycus burjensis*, together with a wide variety of arthropod scratch marks, such as *Dimorphichnus* cf. *obliquus* and *Monomorphichnus* isp. A. Worm structures, such as *Planolites beverleyensis*, *Planolites montanus* and *Palaeophycus tubularis* are also recorded as less conspicuous elements. *Phycodes* isp., *Heminthoidichnites tenuis, Bergaueria sucta*, and *Gordia marina* may be present locally. This assemblage is typically present in thinly bedded current-ripple cross-laminated very fine- to fine-grained sandstone and thicker-bedded trough cross-stratified fine-grained sandstone which occur within heterolithic intervals characterized by flaser-, wavy-, and lenticular-bedded fine- and very fine-grained sandstone and siltstone. These heterolithic deposits occur within and above the interval of relatively large tidal-dune and bar deposits hosting the *Arenicolites* assemblage. The *Cruziana salomonis* assemblage occurs in the lower interval of the Zerqa Ma'in section, the middle interval of the Wadi Qunai section and the upper interval of the Wadi Uhaymir and Wadi Issal sections within the Hanneh Member. Degree of bioturbation (BI ranges between 1–2) and density on bedding planes (BP-BI 1–2) in the deposits containing the *Cruziana salomonis* assemblage is generally low.

This assemblage is dominated by the grazing, feeding and resting structures of trilobites and other arthropods with subordinate presence of worm structures. The tiering structure consists of shallow grazers and deposit-feeding arthropods commonly associated with worm structures, such as *Palaeophycus*, *Planolites,* and *Phycodes. Rusophycus burjensis* can reach deep interfacial surfaces and it may be the only ichnotaxon present at the base of some through cross-bedded sandstone beds which record sedimentation in channels within the tidal-bar sand complex (e.g., Zerqa Ma'in). The highest diversity of trace fossils, however, occurs in the finer-grained deposits recording the bottomsets of tidal dunes and in the low-energy areas between the dunes.

Rusophycus aegypticus *assemblage*.—The *Rusophycus aegypticus* assemblage is an arthropod-dominated suite composed of *R. aegypticus* and *Cruziana jordanica*. These horizontal structures are cross-cut by *Skolithos linearis*. This assemblage is preserved at the base of wave-ripple cross-laminated very fine- to fine-grained sandstone interbedded with siltstone. The *Rusophycus aegypticus* assemblage is present in the upper interval of the Hanneh Member in the Wadi Umm Jafna section. This assemblage records locomotion and resting traces of arthropods, most likely small trilobites, representing shallow-tier structures. Degree of bioturbation in the deposits containing the *Rusophycus aegypticus* assemblage is very low, most deposits look like unbioturbated on cross-sectional view (BI 0–1) and density on bedding planes is low (BPBI 1–2).

Plowings of *Cruziana jordanica* grading into *R. aegypticus* are clearly oriented on the sandstone sole suggesting control by dominant currents. Low diversity may indicate stressed conditions, most likely freshwater imput and fluctuating energy conditions. Integration of sedimentologic and ichnologic evidence suggests deposition in a delta-front setting affected by waves and fluvial discharge with subordinate tidal action.

Cruziana problematica *assemblage*.—The *Cruziana problematica* assemblage consists of *Cruziana problematica, Rusophycus carbonarius*, and *Rusophycus* isp. preserved as positive hyporelief in parallel-laminated very fine- to fine-grained sandstone (Fig. 11.1–11.6). This assemblage occurs at a distinctive stratigraphic level near the boundary between the Hanneh Member (Burj Formation) and the overlying Umm Ishrin Formation in Wadi Al Hisa but has also been recorded in the Umm Ishrin Formation itself.

This assemblage is represented by locomotion and resting trace fossils of small arthropods. The large undetermined *Rusophycus* were emplaced at a later time and represent a different bioturbation event. *Cruziana problematica* and *Rusophycus carbonarius* are bedding-plane parallel trace fossils with no disturbance of the primary sedimentary fabric. Density on bedding planes is low to moderate (BP-BI 3–4). All the components of this assemblage are very shallow-tier structures.

The very low diversity of the *Cruziana problematica* assemblage reveals increased environmental stress. Integration of sedimentologic and ichnologic evidence suggests that this assemblage reflects brackish-water conditions of proximal delta-front environments which are recorded in the boundary interval of the Hanneh Member and the Umm Ishrin Formation. The *Cruziana problematica* assemblage in the Umm Ishrin Formation is present in even more proximal deltaic facies and is thought to record the ability of arthropods to periodically migrate inland due to amphidromy or via salt-water wedges (Maples and Archer, 1989; Buatois et al., 2005).

Archaeonassa fossulata *assemblage*.—The *Archaeonassa fossulata* assemblage consists of monospecific suites of this ichnospecies (Fig. 7.1). It is present at the top of current- and wave-ripple cross-laminated very fine- to fine-grained sandstone. Climbing ripples, flaser bedding, mudstone drapes, and syneresis cracks are also present. Sedimentologic evidence indicates tidal action and subordinate wave influence. This assemblage occurs in the upper interval of the Hanneh Member at the Wadi Qunai section. *Archaeonassa fossulata* represents superficial grazing structures of detritus feeders. This ichnospecies is preserved on

bedding planes, and no disturbance of the primary sedimentary fabric is observed. Density on bedding planes is high (BP-BI 3–4).

The *Archaeonassa fossulata* assemblage characterizes breaks in sedimentation and low-energy conditions. Its monospecific nature is consistent with stressed environments. This scenario is also supported by the presence of syneresis cracks which are interpreted to be formed due to freshwater input. Experimental work has produced similar cracks by varying the concentration of salt in the fluid (e.g., Weiss, 1958; Plummer and Gostin, 1981). As indicated by Jensen et al. (2006), the prevalence of this ichnotaxon in lower Paleozoic rocks could be a result of favorable preservation of surface traces as a consequence of limited sediment mixing. The *Archaeonassa fossulata* assemblage characterizes prodelta environments subjected to important freshwater discharge.

IMPLICATIONS FOR *CRUZIANA* STRATIGRAPHY

Cruziana and *Rusophycus* have been used as tools in biostratigraphy, especially in lower Paleozoic strata of Gondwana (e.g., Crimes, 1970; Seilacher, 1970, 1990, 1992; Pickerill et al., 1984; Orłowski, 1992; Mángano and Buatois, 2003b; Buatois and Mángano, 2011). The morphology of these structures can be quite complex and is strongly controlled by the anatomy and burrowing technique of their producers, most likely trilobites for the lower Paleozoic. According to Seilacher, (1970, 1990, 1992), the distinctive fingerprints of these structures is the so-called "claw formula" that can be related to a group of organisms (not necessarily one species but a group of closely related species). This is debatable as there is no proof that the morphology of the terminal segment (or set of spines on walking appendages) is a character with evolutionary significance (e.g., synapomorphy). However, the claw fomula in combination with behavioral traits, in particular the burrowing technique, can certainly offer a more solid ground. On the other hand, arthropod structures such as *Cruziana* and *Rusophycus* are commonly the only paleontologic evidence available given the absence of body fossils in many lower Paleozoic sandstone-dominated successions. However, a one-to-one correlation between trilobite species and *Cruziana* ichnospecies cannot be established. The most likely correlation is between certain ichnospecies of *Cruziana* and a number of probably phylogenetically related trilobite species. The stratigraphic resolution of trilobite trace fossils is lower than that of trilobite body fossils.

One major problem with *Cruziana* stratigraphy is that several *Cruziana* (and *Rusophycus*) ichnospecies are only known from their type localities or from a few localities (Buatois and Mángano, 2011). This is further complicated by the fact that independent chronostratigraphic evidence (e.g., body fossils, radiometric datings) is absent in many of these units.

The ichnospecies of *Cruziana* and *Rusophycus* from the Cambrian of Jordan described in this paper have direct implications in current ichnostratigraphic schemes and allow testing and refining the *Cruziana* stratigraphy paradigm. Seilacher (1990) noted that *Cruziana salomonis* occurs in the Zerqa Ma'in outcrops of Jordan in strata containing trilobites regarded as indicative of a late early Cambrian age (Series 2). However, the trilobites of these strata have been re-evaluated in detail by Elicki and Geyer (in press) who conclude that they indicate the lower part of Cambrian Stage 5 (Series 3), which corresponds approximately to a lower middle Cambrian age of the traditional Cambrian subdivision (e.g., Rushton and Powell, 1998). Seilacher (1990) also regarded *R. aegypticus* as "lower Cambrian." This ichnotaxon is known from strata of the Sinai Peninsula and the Eastern Desert of Egypt (interpreted by Seilacher, 1990 as "lower Cambrian" in age) and the middle Cambrian of southern Jordan (*C. aegyptica* in Schneider et al., 2007 and Amireh et al., 1994). All occurrences of *R. aegypticus* are mono- or paucispecific assemblages (intergrading with *C. jordanica*). Seilacher outlined that he never observed co-occurrences with *Cruziana salomonis* in Sinai and the Eastern Desert and therefore suggested that *R. aegypticus* could represent a slightly older form. Although not forming part of the same trace-fossil assemblage, both ichnospecies are present in the same stratigraphic interval in the Wadi Qunai and Wadi Umm Jafna sections of the Dead Sea area. The fact that *Cruziana salomonis* and *R. aegypticus* form distinct assemblages (i.e., they are never associated) is interpreted as resulting from different ecologic requirements of the tracemakers rather than the age of the rocks. Our study demonstrates that *Cruziana salomonis* and *R. burjensis* are actually early middle Cambrian in traditional terms (stage 5) in its type locality, Zerqa Ma'in. The occurrence of *R. aegypticus* and *C. jordanica* in the Hanneh Member, well above the strata containing Cambrian Stage 5 trilobites, also provides evidence that these ichnotaxa are middle Cambrian in age. More precise dating of the occurrences in Egypt is necessary to demonstrate that these forms extend into the lower Cambrian.

CONCLUSIONS

Eleven trace-fossil assemblages have been identified in the Hanneh Member (Cambrian Stage 5) of the Burj Formation and the lower part of the Umm Ishrin Formation of Jordan, reflecting multiple responses of the benthic fauna to environmental factors in a transgressive-regressive succession.

The *Arenicolites* isp. and *Diplocraterion* isp. assemblages are present in transgressive tidal dunes and bars. The *Rosselia* isp. assemblage occurs in areas between tidal dunes. The *Cruziana salomonis* assemblage is present in channels within tidal-bar complexes, bottomsets of tidal dunes, and interdune areas. The *Gordia marina* assemblage occurs between dune patches. The *Gyrolithes polonicus* assemblage characterizes firm substrates below the maximum flooding surface. The *Bergaueria sucta*, *Archaeonassa fossulata*, *Rusophycus aegypticus*, and *Cruziana problematica* assemblages occur in different subenvironments of the progradational delta.

Based on independent biostratigraphic evidence (e.g., extensively studied trilobites in strata below the trace fossil-bearing deposits), *Cruziana salomonis* and *Rusophycus burjensis* occur early in Cambrian stage 5 in their type locality which is best interpreted to correspond to the traditional early middle Cambrian in their type locality. In addition, *Cruziana jordanica* and *Rusophycus aegypticus* do also occur in Cambrian stage 5 in Jordan and may co-exist in terms of stratigraphic distribution with *C. salomonis* and *R. burjensis*.

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